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THE CRANIAL MORPHOLOGY
OF RHYACOTRITON
OLYMPICUS OLYMPICUS (GAIGE)

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THE CRANIAL ANATOMY AND KINESIS
OF THE BIRD SNAKE
THELOTORNIS CAPENSIS (SMITH)

BY

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THE CRANIAL MORPHOLOGY OF RHYACOTRITON OLYMPICUS OLYMPICUS (GAIGE)

by

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(With 13 text-figures)

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ABSTRACT

This investigation consists of a systematic description of the cranial anatomy of *Rhyacotriton o. olympicus*. The most outstanding feature of *Rhyacotriton* is the absence of the nasals, which distinguishes it from the remaining two genera of the *Ambystomidae*. The lacrimal is present as a separate bone and contains a canal for the ductus nasolacimalis. The well developed stylus columellae is the only representative of the sound-conducting apparatus. The skull is probably monimostylic as the processus ascendens and the processus oticus are fused to the chondrocranium.

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INTRODUCTION

Any research work on urodeles is notoriously difficult. The difficulty is not due to the complexity of structure but to the problem of gauging the phylogenetic position of the group. It is extremely difficult to distinguish primitiveness from degeneration or from a secondary achievement of simplicity which results from arrested development or neoteny, which latter is probably manifested by all members of the group. In view of these difficulties it is deemed advisable to refer to De Villiers's work (1944) in which he discusses these very problems encountered in the evaluation of urodele morphology.

It is generally argued that since neoteny is in itself a specialization, or in terms of the Viennese school (Abel and others, 1929) an orthogenesis, those urodeles that are least neotenic are least specialized, but it is a matter of extreme difficulty to distinguish neotenic simplicity of organization from primitiveness; this is notoriously the case in urodeles, or as the problem is sometimes put: all urodeles are infected with neoteny. Although for some reason or other it is generally tacitly assumed that the Asiatic urodeles, such as the *Hynobiidae*, are least neotenic, American families have not been specially investigated with the view to demonstrating the degree of neoteny displayed.

In 1917 Mrs. H. T. Gaige described a new species of salamander from Washington State as *Ranodon olympicus*. She considered the discovery of a species of *Ranodon* from North America as particularly noteworthy, since, up to that time, that genus had been known only from a single species, *Ranodon sibiricus*, from eastern Siberia and north-eastern China. In 1920, however, Dunn concluded that this species was generically distinct from *Ranodon*, and he created the genus *Rhyacotriton* for it. This conclusion has been accepted by all subsequent workers. Stebbins (1951) recognizes two subspecies: *R. o. variegatus* and *R. o. olympicus*.

Ambystoma, *Dicamptodon* and *Rhyacotriton* are the only genera of the family *Ambystomidae*, which is confined to the Nearctic Region, but whereas *Ambystoma* is distributed widely throughout its central and southern parts, *Rhyacotriton* is confined to the coastal region west of the Cascade Mountains, between western Washington State and north-western California. *Dicamptodon* has more or less the same distribution, but its range extends slightly further north and south than that of *Rhyacotriton*; moreover, it has an outlier in Idaho (Stebbins, 1951).

Previous investigations have dealt chiefly with the suspensorial region of this species, with observations made by Eaton (1933) and the contribution by De Villiers (1938) who regards *Rhyacotriton* as monimostylic. Thus the occurrence of streptostyly (Eaton, 1933) would appear to be unlikely. The present investigation is mainly a descriptive account of the cranial morphology of the genus.

MATERIAL AND TECHNIQUE

Two adult male specimens, which were collected along the banks of the Calawah River, a half mile north of Forks, Washington State, and kindly supplied by the Chicago Natural History Museum, were microtomed. Measurements from snout to tip of tail were 90.0 mm. and 76.9 mm.; from snout to vent 51.3 mm. and 46.6 mm. respectively. The severed heads of the specimens, which were preserved in formalin, were decalcified in either Ebner's solution or in Mueller's fluid. The latter proved to be far superior. They were bulk-stained in borax-carmin, embedded and sectioned transversely at a thickness of 15μ and counterstained in Azan solution.

Graphic reconstructions were made from projection drawings of the cross-sections according to Pusey's method (1939).

ACKNOWLEDGEMENTS

Grateful acknowledgement is made to the Chicago Natural History Museum for supplying the specimens used in this investigation. My thanks are also due to the C.S.I.R. for their financial assistance during the past two years. I would like to express my appreciation to Professor C. A. du Toit, under whose direction the work has been carried out, and to Professor C. G. S. de Villiers for his kind interest.

STRUCTURE OF THE NASAL CAPSULE

The cartilaginous nasal capsule houses the nasal organ. The external naris passes through the fenestra narina, and the fenestra basalis nasi serves as an opening for the choana into the oral cavity. In addition, the nasal capsule is perforated by a number of conspicuous fenestrae which will be discussed later. Certain parts of the nasal organ are devoid of cartilage, but become enclosed by membrane bones.

The fenestra narina, homologous to the fenestra endonarina communis (Jarvik, 1942) is a large, laterally situated opening in the anterior paries nasi, which cannot be seen dorsally as it can in some other forms (Fig. 1). It is bounded anteriorly by the cartilago cupularis and posteriorly by the broad cartilago retronarina. The cartilago obliqua forms its dorsal border, separating the fenestra dorsalis nasi from the fenestra narina. Ventro-laterally it is separated from the fenestra basalis nasi by the cartilago infranarina or lamina nario-choanalis (Jarvik, 1942).

In all larval stages the fenestra narina is situated terminally; there has probably been some shifting involved during ontogeny. The lateral position of the fenestra narina is clearly influenced by the formation of the cartilago cupularis (Higgins, 1920). The anterior external naris leads from the main chamber of the nasal sac and opens to the exterior in the anterior corner of the fenestra narina. In addition the large fenestra narina accommodates the muscles of the mechanism controlling the intake of air; it is accompanied by the lateral nasal artery, as well as the glandula nasalis externa. Through the posterior corner of the fenestra narina the ductus nasolacimalis leaves the nasal cavity and is continued backwards dorso-posteriorly through a foramen in the septomaxillary (Fig. 4).

In two known cases, those of *Plethodon* (Lapage, 1928) and *Spelerpes* (Stadtmüller, 1936) the fenestra narina is divided by a cartilaginous band. The external naris therefore has a separate opening, the fenestra endonarina anterior. The ductus nasolacimalis passes through the fenestra endonarina posterior (Jarvik, 1942).

The fenestra dorsalis nasi is a broad five-sided gap in the postero-medial portion of the roof (planum tectale, Higgins, 1920) of the nasal capsule. It is medially bounded by the columella ethmoidalis (Fig. 1), posteriorly by the cartilago antorbitalis, postero-laterally by the planum conchale, antero-laterally by the cartilago obliqua and anteriorly by the cartilago cupularis. The fenestra transmits branches of the ramus medialis nasi of the nervus profundus, as well as the medial nasal blood-vessels. Anterior to the fenestra dorsalis nasi, foramina are encountered in the cartilago cupularis; through some of these, small nerves may be seen passing. The incompleteness of the urodelan nasal capsule is ascribed by some authors to incomplete chondrification (De Beer, 1937), whereas others, e.g. Higgins (1920) are of opinion that it is due to resorption of cartilage. Jarvik (1942) gives a detailed review of the literature on this subject and concludes that the heavily fenestrated nasal capsule of the adult urodele is, in a large measure, due to resorption of cartilage during metamorphosis. In *Rhyacotriton* the left nasal capsule has a fenestra dorsalis nasi, considerably smaller in size than that of the right side.

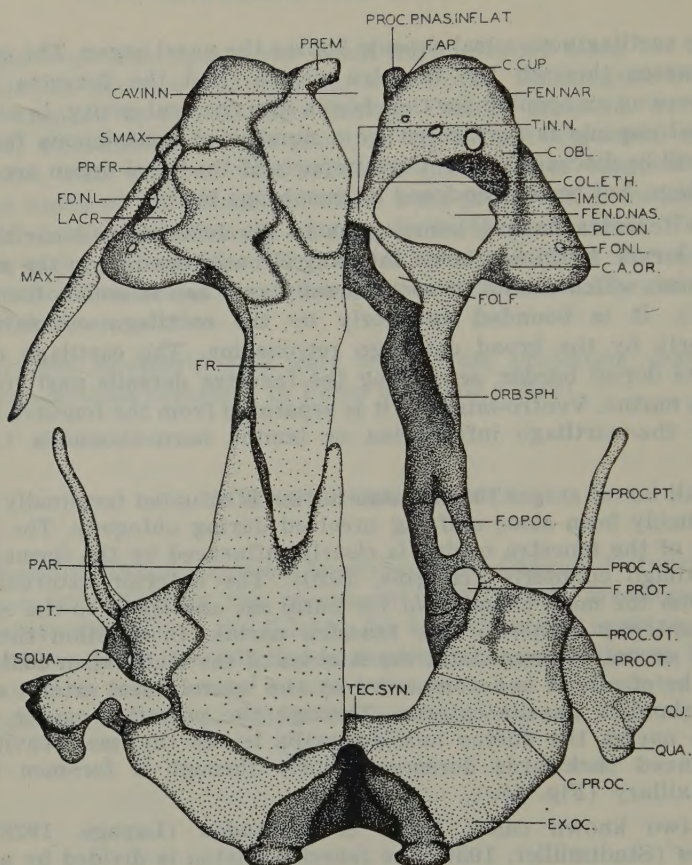


Figure 1.

Graphic reconstruction of the skull x approx. 14.8. Dorsal view.
 C.A.OR., cartilago antorbitalis; CAV.IN.N., cavum internasale;
 C.CUP., cartilago cupularis; C.OBL., cartilago obliqua; COL.ETH.,
 columella ethmoidalis; C.PR.OC., cartilago prootico-occipitalis;
 EX.OC., exoccipital; F.AP., foramen apicale; F.D.N.L., foramen for
 ductus nasolacimalis; FEN.D.NAS., fenestra dorsalis nasi; FEN.
 NAR., fenestra narina; F.OLF., foramen olfactorium; F.O.N.L.,
 foramen orbitonasale laterale; F.OP.OC., foramen optico-oculomo-
 torium; F.PR.OT., foramen prooticum; FR., frontal; IM.CON., im-
 pressio conchalis; LACR., lacrimal; MAX., maxillary; ORB.SPH.,
 orbitosphenoid; PAR., parietal; PL.CON., planum conchale; PREM.,
 premaxillary; PR.FR., prefrontal; PROC.ASC., processus ascendens;
 PROC.OT., processus oticus; PROC.P.NAS.INF.LAT., processus
 praenasalis inferior lateralis; PROC.PT., processus pterygoideus;
 PROOT., prootic; PT., pterygoid; Q.J., quadratojugal; QUA., qua-
 drate; S.MAX., septomaxillary; SQUA., squamosal; TEC.SYN.,
 tectum synoticum; T.IN.N., tectum internasale.

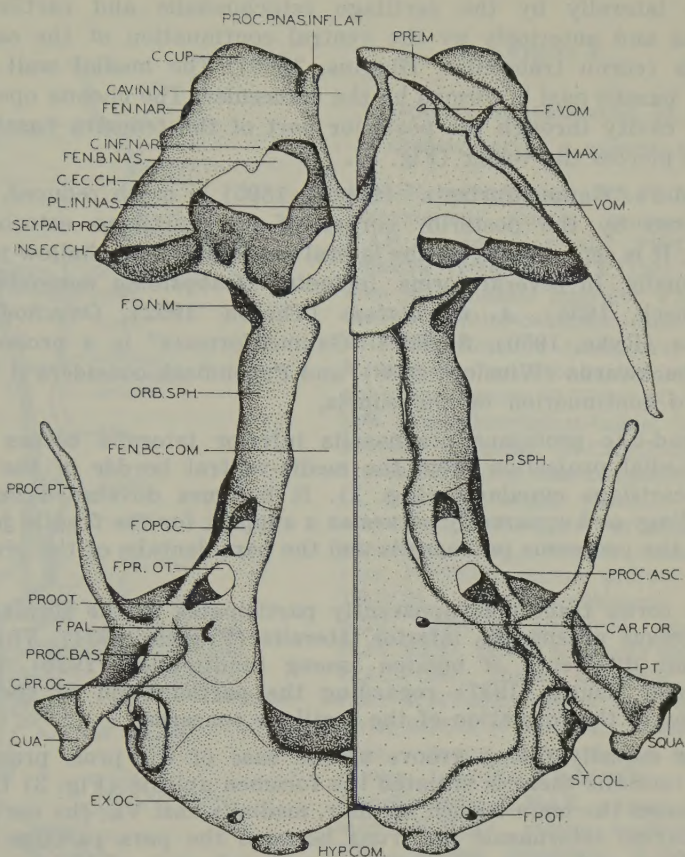


Figure 2.

Graphic reconstruction of skull x approx. 14.8. Ventral view.
 CAR.FOR., carotid foramen; CAV.IN.N., cavum internasale; C.CUP., cartilago cupularis; C.EC.CH., cartilago ectochoanalis; C.INF.NAR., cartilago infranarina; C.PR.OC., cartilago prootico-occipitalis; EX.OC., exoccipital; FEN.BC.COM., fenestra basicanialis communis; FEN.B.NAS., fenestra basalis nasi; FEN.NAR., fenestra narina; F.O.N.M., foramen orbitonasale mediale; F.O.P.O.C., foramen optico-oculomotorium; F.PAL., foramen palatinum; F.P.OT., foramen postoticum; F.P.R.OT., foramen prooticum; F.VOM., foramen in vomer; HYP.COM., hypochordal commissure; INS.EC.CH., incisura ectochoanalis; MAX., maxillary; ORB.SPH., orbitosphenoid; PL.IN.NAS., planum internasale; PREM., premaxillary; PROC.ASC., processus ascendens; PROC.BAS., processus basalis; PROC.PNAS. INF.LAT., processus praenasalis inferior lateralis; PROC.PT., processus pterygoideus; PROOT., prootic; P.SPH., parasphenoid; PT., pterygoid; QUA., quadrate; SEY.PAL.PROC., Seydel's palatal process; SQUA., squamosal; ST.COL., stylus columellae; VOM., vomer.

The fenestra basalis nasi is situated in the solum nasi and is bounded laterally by the cartilago ectochoanalis and cartilago infranarina and anteriorly by the ventral continuation of the cartilago cupularis (cornu trabeculae, Higgins, 1920). The medial wall of the fenestra basalis nasi is formed by the trabeculae. The choana opens into the oral cavity through the posterior part of the fenestra basalis nasi and also pierces the vomer (Fig. 2).

Seydel's "Gaumenfortsatz" (Seydel, 1895) is much reduced, and is represented by the posterior corner of the cartilago ectochoanalis (Fig. 2). It is separated from the lateral nasal wall by a shallow incisura ectochoanalis. In several forms, including *Ambystoma macrodactylum* (Papendieck, 1954), *A. maculatum* (Theron, 1952), *Onychodactylus japonicus* (Ryke, 1950), Seydel's "Gaumenfortsatz" is a process projecting backwards (Winslow, 1898), and Papendieck considers it to be a backward continuation of the cupola.

A rod-like processus praenasalis inferior lateralis occurs as an antero-medial projection from the medio-ventral border of the dome-shaped cartilago cupularis (Fig. 1). It becomes dovetailed onto the premaxillary and apparently serves as a support for the fragile junction between the processus praenasalis and the pars dentalis of the premaxillary.

The cornu trabeculae apparently participates in the formation of the processus praenasalis inferior lateralis (Francis, 1934). There has been some difference of opinion among Stadtmüller (1936), Francis (1934) and Chung (1931) regarding the participation of the cornu trabeculae in the formation of the cartilage concerned.

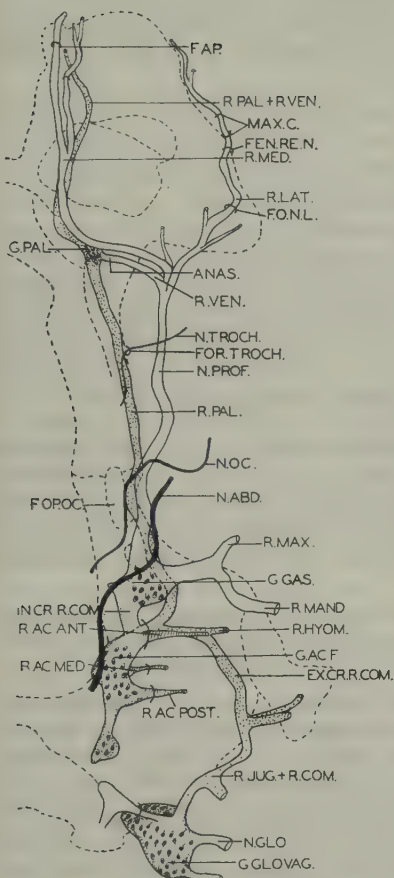
In a dorsally facing groove at the base of the proc. praenasalis inferior lateralis there is situated the foramen apicale (Fig. 3) through which passes the main branch of the r. medialis nasi Va; the nerve ends in the cavum internasale and runs between the pars palatina of the premaxillary and the nasal capsule. Another branch of the r. medialis nasi perforates the cartilago cupularis, dorsally to the foramen apicale.

The absence of a median unpaired processus praenasalis superior medius is clearly influenced by the lack of development of a tectum internasale. Corresponding conditions are found in *Ambystoma maculatum* (Theron, 1952) and in *A. macrodactylum* (Papendieck, 1954). In *Onychodactylus japonicus* (Ryke, 1950) the processus praenasalis superior medius is broad and projects forwards from the tectum internasale.

It is difficult to determine the exact homology of the small foramen in the ventro-lateral part of the planum conchale; considering its relationship to the structures in its immediate vicinity, it would seem to be the fenestra retrorhinaria (Fig. 5). After the r. lateralis nasi separates from the r. ophthalmicus profundus in the anterior part of the orbit, it runs laterally and then lies above the cartilago antorbitalis. In this position it gives off two ramuli which supply the skin over the upper jaw. The main nerve then penetrates the nasal capsule dorso-laterally through the foramen orbitonasale laterale (Figs. 3 and 6). It runs inside the capsule for some distance and upon emerging from it enters a canal in the pars facialis of the maxillary (Fig. 3). It then bifurcates and finally terminates laterally to the nasal capsule.

Figure 3.

Graphic reconstruction of the
cranial nerves x approx. 14.8.



ANAS., anastomosis; EX.CR.R.COM., extracranial ramus communicans; F.AP., foramen apicale; FEN.RE.N., fenestra retronarina; F.O.N.L., foramen orbitonasale laterale; F.OP.OC., foramen optico-oculomotorium; FOR.TROCH., foramen trochleare; G.A.C.F., ganglion acustico-faciale; G.GAS., ganglion Gasseri; G.GLO.VAG., ganglion glossopharyngeus-vagus; G.PAL., palatine ganglion; IN.CR.R.COM., intracranial ramus communicans; MAX.C., maxillary canal; N.ABD., nervus abducens; N.GLO., nervus glossopharyngeus; N.OC., nervus oculomotorius; N.PROF., nervus profundus; N.TROCH., nervus trochlearis; R.AC.ANT., ramus acusticus anterior; R.AC.MED., ramus acusticus medialis; R.AC.POST., ramus acusticus posterior; R.HYOM., ramus hyomandibularis; R.JUG. + R.COM., ramus jugularis + ramus communicans; R.LAT., ramus lateralis; R.MAND., ramus mandibularis; R.MAX., ramus maxillaris; R.MED., ramus medialis; R.PAL., ramus palatinus; R.PAL. + R.VEN., ramus palatinus + ramus ventralis; R.VEN., ramus ventralis.

The fenestra lateralis nasi (Jarvik) is supposed to be an opening for housing the lateral bulge of the nasal sac. His more recent investigations have convinced Jarvik that one should distinguish between a fenestra retronarina and a fenestra lateralis nasi in more specialized urodeles. Chung's identification of the fenestra retronarina with the fenestra infraconchalis (Francis), fenestra lateralis nasi (Jarvik) and possibly the foramen epiphaniale (Goodrich) has caused some confusion. Owing to the absence of an opening in the lateral nasal wall in *Onychodactylus fisherii* and *Hynobius nebulosus*, Jarvik maintains that in higher urodeles the fenestra lateralis nasi is a new formation, and that it is situated somewhat further forward.

The fenestra retronarina of *Rhyacotriton* is a small opening lying more postero-ventrally on the planum conchale than in other genera. Furthermore, the fenestra retronarina no longer houses the lateral bulge of the nasal sac and serves to transmit only the r. lateralis nasi. Similar conditions obtain in *Diemictylus pyrrhogaster*, *D. ensicauda* (Chung) and

Plethodon glutinosum (Winslow). Jarvik points out that the fenestra retrorhinaria agrees essentially with the fenestra endorhinaria posterior in the postero-ventral part of the lateral nasal wall of the crossopterygian, *Porolepis*. The inevitable conclusion is, therefore, that *Rhyacotriton* belongs to the less advanced urodeles.

In several species the r. lateralis nasi passes through the fenestra lateralis nasi. Such forms are *Ambystoma macrodactylum* (Papendieck, 1954), *A. maculatum* (Theron, 1952), and *Salamandra* (Francis, 1934).

Several foramina orbitonasalia lateralia may occur in the planum conchale. Papendieck found that the homology of these foramina was difficult to determine. Great variation occurs in different species of the same genus and sometimes even in the same species. In the sections of *Ambystoma maculatum* and of *Onychodactylus japonicus* I have found that one of the foramina orbitonasalia lateralia transmits the r. lateralis nasi. The remaining foramina serve for the passage of bloodvessels. Apparently the number of foramina also varies: there are three in *Ambystoma maculatum* (Theron, 1952), four in *Hynobius naevius* (Chung, 1931), five in *Hynobius retardatus* (Chung, 1931), four or more in *Onychodactylus japonicus* (Ryke, 1950) and several in *Salamandra* (Stadtmüller, 1924). In *Rhyacotriton* there is a single foramen orbitonasale laterale (Fig. 1) as in *Diemictylus pyrrhogaster*, *D. ensicauda* (Chung 1931), *Triturus* (Stadtmüller, 1936) and *Plethodon glutinosum* (Winslow, 1898).

According to Chung (1931) the incisura ectochoanalis is confluent with the fenestra retrorhinaria in *Hynobius tsushimensis*, *Hynobius leechi* and *Pseudosalamandra*, but this is not the case in *Rhyacotriton*.

The foramen orbitonasale mediale is situated in the medial part of the cartilago antorbitalis, being a comparatively large opening through which the r. medialis nasi and the r. ventralis nasi enter the nasal capsule; it also transmits the medial nasal bloodvessels. The musculus obliquus superior is attached to that part of the cartilago antorbitalis which forms the ventral border of the foramen orbitonasale mediale. Similar conditions obtain in *Onychodactylus* (Ryke, 1950). The r. ventralis nasi anastomoses with the r. palatinus VII at the palatine ganglion (Fig. 3) immediately after entering the nasal capsule and the mixed nerve pierces the vomer (Fig. 2).

The impressio conchalis (Stadtmüller, 1924) is a longitudinal indentation in the planum conchale, leading backwards from the fenestra rhinaria. Jarvik maintains that it exists for the reception of the ductus nasolacrimalis. According to De Beer (1937) the impressio conchalis represents an exceedingly rudimentary concha nasalis. The crista rostrocaudalis (Fig. 6) apparently follows the course of the impressio conchalis. The crista rostrocaudalis does not fuse ventrally with the cartilago ectochoanalis as it does in *Ambystoma macrodactylum* (Papendieck, 1954) and in *A. maculatum* (Theron, 1952).

The conspicuous cavum internasale replacing the septum nasi is an important feature of the ethmoidal region. The internasal septum has disappeared in most urodeles, and posteriorly the only remains of it, according to some workers, are the planum and the tectum internasale, also known as the ethmoid plate (Winslow, 1898). A true nasal septum is present in *Salamandra maculosa* (De Beer, 1937) and *Siren lacertina* (Wiedersheim, 1877) where it lies in the position of the cavum internasale. The latter is bounded laterally by the medial walls of the nasal

capsules, posteriorly by the planum and tectum internasale, but ventrally it lacks a floor. The nasal capsules are, therefore, completely separate. According to Stadtmüller (1936) the cavum internasale is a secondary characteristic. The glandula intermaxillaris (Fig. 4) occupies the entire cavum internasale, and according to Seifert (1932), the contents of this ramified tubular gland is discharged through short ducts, not only into the oral cavity ventrally, but also dorsally onto the skin.

A fenestra praecerebralis (fenestra ethmoidalis, Higgins, 1920) is present as in *Onychodactylus* (Ryke, 1950), *Triturus* (Born, 1876), *Diemictylus* (Higgins, 1920) and *Euproctus* (Stadtmüller, 1936).

The foramen olfactorium (Figs. 2 and 6) is a particularly wide perforation in the wall separating the cranial from the nasal cavity. The foramen is bounded dorsally by the cartilago antorbitalis and ventrally by the planum internasale (Fig. 6).

MEMBRANE BONES OF THE ETHMOIDAL REGION

The exposed parts of the nasal organ, particularly in the fenestra dorsalis nasi and in the fenestra basalis nasi, are protected by the dermal bones occurring in the ethmoidal region. Laterally the nasal organ is completely exposed through the fenestra narina, and a great part of the glandula intermaxillaris is devoid of skeletal protection. Those bones covering the nasal organ are the premaxillary, maxillary, lacrimal, prefrontal, septomaxillary and the vomer.

Anteriorly, both premaxillaries are in syndesmosis. Grote (1926) states that Born described an intervening unpaired piece of bone in *Triturus* by means of which the premaxillaries are united. Grote, however, could locate no such bone in *Siredon pisciformes* (*Ambystoma tigrinum*). Separate premaxillaries also occur in *Ambystoma macrodactylum* (Papendieck, 1954) and *Onychodactylus japonicus* (Ryke, 1950). The premaxillary consists of two major parts: the processus praenasalis and the pars dentalis. The term pars palatina as described for *Salamandra maculosa* by Stadtmüller (1924), was introduced by O. Hertwig (1874) as the third portion of the premaxillary; it forms a bony palate. In *Ambystoma tigrinum* (Grote, 1926) there is no trace of the pars palatina, in *Rhyacotriton* and *Ambystoma macrodactylum* it is rudimentary but in *Onychodactylus* (Ryke, 1950) it is better developed.

The processus praenasalis ascends as a thin bony strip closely applied to the inner surface of the median wall of the cartilago cupularis; dorsally it possesses a long posteriorly directed plate. It covers a great part of the cartilago cupularis and also of the cavum internasale. It overlaps the frontal and terminates abruptly, without being produced into a posterior tip as in *Ambystoma maculatum* (Theron, 1952). It remains quite free from the prefrontal and functionally replaces the nasal. Francis (1934) compares it with the short processus praenasalis in some *Urodela*. Jarvik (1942) reaches the conclusion that it has undergone progressive development. Although the nasals are not present as separate bones in *Rhyacotriton* (Noble, 1931) it could be assumed that they are fused with the premaxillaries. As mentioned above the premaxillary contains a socket into which the processus praenasalis inferior lateralis fits. The process probably has the function of strengthening the weak connexion between the processus praenasalis

and the pars dentalis; the latter forms the anterior portion of the arch of the upper jaw. The teeth borne on the pars dentalis are of the pleurodont type and are monocuspid in shape (Francis, 1934).

The maxillary completes the upper jaw laterally. The bone has three parts: the pars palatina, pars facialis and pars dentalis. The pars palatina is applied ventrally to the cartilago infranarina and to the cartilago ectochoanalis (Fig. 2). The pars facialis overlaps the lacrimal and completely covers the fenestra retronarina. Anterior to the fenestra retronarina a fairly long canal located in the pars facialis serves to transmit the r. lateralis nasi on its way to the skin (Fig. 3). Ventrally the pars facialis passes into the pars dentalis which extends into the orbital region by means of the processus maxillaris posterior. On the pars dentalis there is located a single row of teeth medially to which numerous isolated anlagen are observed. The processus maxillaris posterior stretches caudally and terminates laterally to the processus pterygoideus. This slender projection remains completely separate; the communication with the so-called "lateral extremity of the suspensorium" (Francis) is thus totally lost. In *Onychodactylus* (Ryke, 1950) and *Salamandra* (Francis, 1934) there is a ligamentous connexion between these two structures. In *Ambystoma maculatum* (Theron, 1952) the processus posterior maxillaris is in contact with the processus pterygoideus, and in *Ambystoma macrodactylum* (Papendieck, 1954) they

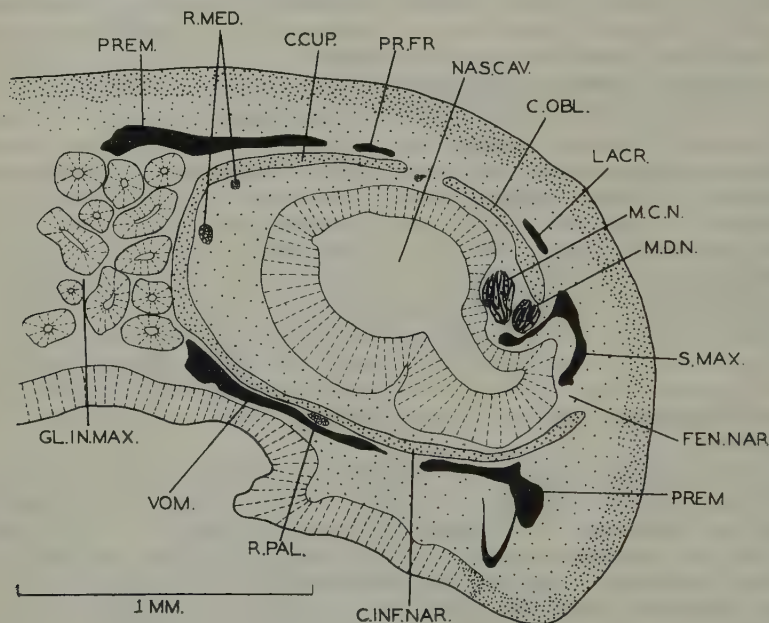


Figure 4.

Transverse section through the region of the septomaxillary.

C.CUP., cartilago cupularis; C.INF.NAR., cartilago infranarina; C.OBL., cartilago obliqua; FEN.NAR., fenestra narina; GL.IN.MAX., glandula intermaxillaris; LACR., lacrimal; M.C.N., musculus constrictor naris; M.D.N., musculus dilatator naris; NAS.CAV., nasal cavity; PREM., premaxillary; PR.FR., prefrontal; R.MED., ramus medialis; R.PAL., ramus palatinus; S.MAX., septomaxillary; VOM., vomer.

approach each other closely and are connected by means of a tenuous ligament.

The lacrimal occurs as a distinct preorbital membrane bone situated dorso-laterally to the planum conchale (Fig. 5). The slender lacrimal extends between the maxillary and the prefrontal, overlapping it posteriorly. It contains part of the canal for the ductus nasolacrimalis; the duct then continues forwards and pierces the septomaxillary. On the right side the lacrimal is attached to the prefrontal at its posterior end only. On the left side the lacrimal remains separate, being entirely surrounded by connective tissue.

In 1877, Wiedersheim described for *Hynobius* (*Ellipsoglossa*) and *Ranodon* a small bone the "Praefrontale II" occupying the typical position of a lacrimal. The Sarasins (1887—1890) homologised this "Praefrontale II" with the "true" lacrimal of *Stegocephalia* and *Amniota*; this conclusion is accepted by Gregory (1920). Stadtmüller (1936) does not accept the homology between the lacrimal and the "Praefrontale II". In forms like *Dicamptodon*, *Rhyacotriton* (Eaton, 1934), *Onychodactylus* (Ryke, 1950), *Gyrinophilus* (Cope, 1889), *Cryptobranchus* (Wiedersheim, 1877) the lacrimal is present, though Gregory (1920) states that most urodeles have lost this bone. Judging from conditions in *Onychodactylus* (De Beer, 1937), *Ambystoma maculatum* (Theron, 1952) in which the prefrontal is penetrated by the ductus nasolacrimalis, it would appear that the lacrimal becomes fused with the prefrontal (De Beer, 1937).

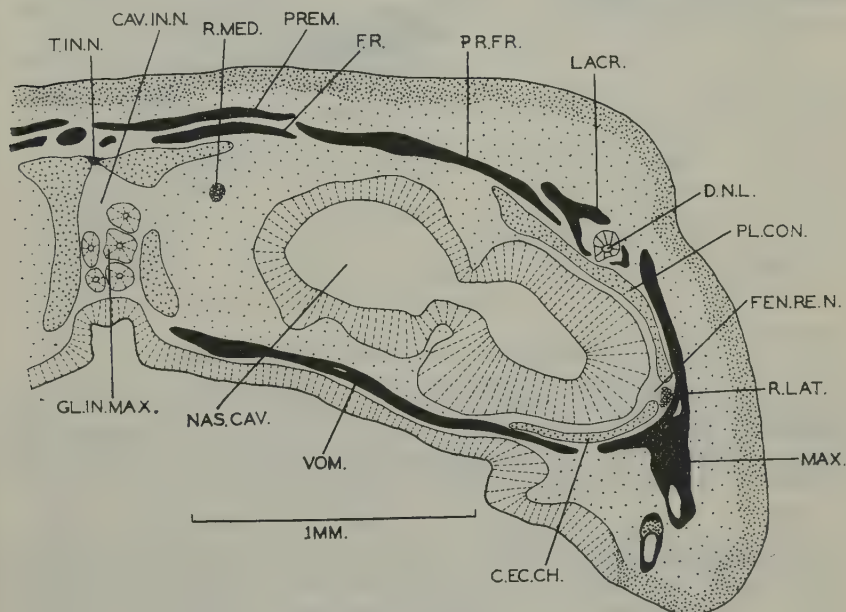


Figure 5.

Transverse section through region of lacrimal.

CAV.IN.N., cavum internasale; C.EC.CH., cartilago ectochoanalis; D.N.L., ductus nasolacrimalis; FEN.RE.N., fenestra retrorinarina; FR., frontal; GL.IN.MAX., glandula intermaxillaris; NAS.CAV., nasal cavity; PL.CON., planum conchale; PREM., premaxillary; PR.FR., prefrontal; R.LAT., ramus lateralis; R.MED., ramus medialis; T.IN.N., tectum internasale; VOM., vomer.

The second preorbital membrane bone, the prefrontal, is largely responsible for covering the fenestra dorsalis nasi. This relatively large bone actually touches the premaxillary, overlays the frontal by means of a posterior, inner projection, and its lateral posterior border is concealed by the lacrimal. A canal for the ductus nasolacrimalis, as described for most salamandrids (Stadtmüller, 1936) does not occur. Stadtmüller (1936) notes that in *Proteus*, *Necturus* and *Siren* the prefrontal is absent. The antero-dorsal border of the orbit is formed by the free posterior edges of the prefrontal and lacrimal.

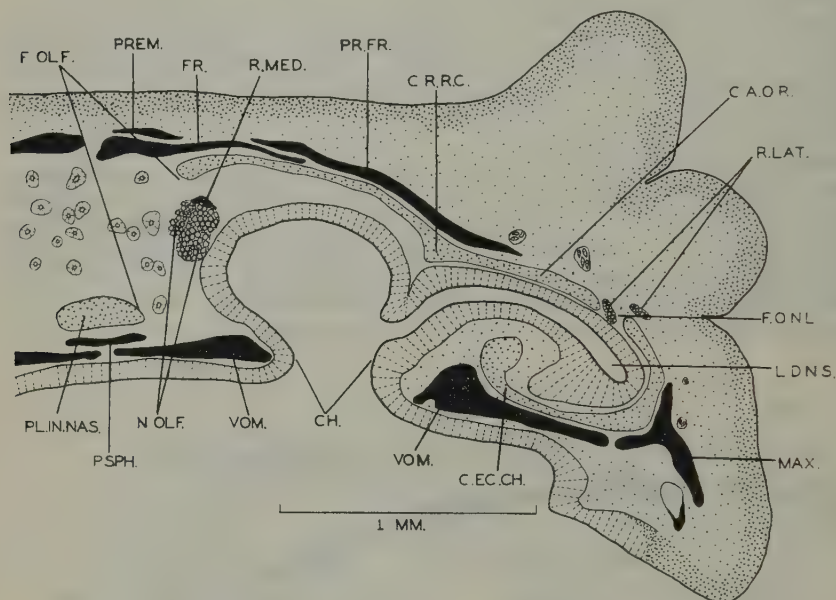


Figure 6.

Transverse section through the foramen olfactorium.

C.A.OR., cartilago antorbitalis; C.EC.CH., cartilago ectochoanalis; CH., choana; CR.R.C., crista rostrocaudalis; F.OLF., foramen olfactorium; F.ONL., foramen orbitonasale laterale; FR., frontal; LD.N.S., lateral diverticulum of nasal sac; MAX., maxillary; N.OLF., nervus olfactorius; PL.IN.NAS., planum internasale; PREM., premaxillary; PR.FR., prefrontal; P.SPH., parasphenoid; R.LAT., ramus lateralis; R.MED., ramus medialis; VOM., vomer.

The septomaxillary (Jarvik's "nariodal") is a small, independent structure situated medial to the pars facialis of the maxillary and anterior to the lacrimal. This gutter-shaped bone occupies the posterior corner of the fenestra narina where it is responsible for the attachment of certain nasal muscles as described by Lapage (1928). The relations of the m. dilatator naris accessorius, m. constrictor naris and m. dilatator naris conform typically to the ambystomid-condition (Fig. 4). Lapage gives a detailed account of the origin and insertion of these muscles and *Rhyacotriton* agrees with *Ambystoma maculatum* (Lapage, 1928). On entering the nasal capsule the ductus nasolacrimalis runs through an excavation between the two posterior arms of the septo-

maxillary which protect it laterally, dorsally and medially. The fenestra exonarina posterior (Jarvik) in the septomaxillary of *Ambystoma maculatum* (Theron, 1952) is absent owing to the absence of a complete canal. The septomaxillary contains a branch of the anterior maxillary artery which conveys blood to the lateral anterior region of the snout and upper jaw (Francis, 1934).

Considerable uncertainty exists regarding the ontogenesis of the septomaxillary. Schmalhausen (1958) confirmed the opinion that the septomaxillary is a dermal bone. He studied the development of this bone in many forms and found that in *Onychodactylus* it has a dermal origin. He concludes that the urodele septomaxillary is homologous with that of *Anura* and *Reptilia*. Schmalhausen is convinced of its homology with the dermal bone enclosing the subnasal part of the infra-orbital canal of bony fishes. Stadtmüller (1936) suggests that a mixed origin of the bone is probable. In *Hynobius nebulosus* he seems to think it is a pure membrane bone. Lapage (1928) and Jarvik (1942) consider it as a cartilage bone. Jarvik is of the opinion that the development of the 'nariodal' is influenced by the posterior part of the ductus nasolacrimalis. Lapage, on the contrary, reaches the conclusion that the septomaxillary provides primarily for the partial origo of a nasal muscle. Barry (1956) provides irrefutable evidence for the membrane origin of the septomaxillary in *Bufo angusticeps*.

The paired vomers are mainly responsible for the dermal protection of the ventral side of the ethmoidal region. The bony palate is formed under the fenestra basalis nasi and the vomer extends anteriorly and touches the premaxillary. A posteriorly directed projection of the vomer underlies the anterior portion of the parasphenoid. Anteriorly the cavum internasale is completely exposed through the anterior palatal fenestra (Jarvik, 1942) which is bounded by the prongs of the vomers. The vomer is pierced by a foramen (Fig. 2) for the r. ventralis V and the r. palatinus VII which supply the mucous membrane of the mouth. Postero-laterally a deep incisure leads to the area bounding the choana; this incisure therefore separates the broad anterior portion. The vomerine teeth are restricted to the postero-medial area and are arranged in two short arched series immediately behind the internal naris. Gaige (1917) and Bishop (1943) used this feature in their diagnosis of the species.

The palatine never occurs as a separate bone in *Urodela*. Investigations by Stadtmüller (1936) show that the palatine becomes fused to the vomer during ontogeny; thus a vomero-palatine is formed. A second view is that of Aoyama (1930) and Wintrebert (1922) who maintain that the palatine disappears during metamorphosis and that a vomero-palatine in *Urodela* therefore does not occur. Jarvik (1942) and Wilder (1920) give a different explanation: in certain *Crossopterygii* the parasphenoidal dental plate corresponds with the vomerine tooth-bearing process of some *Urodela*. In *Ambystoma maculatum* (Theron, 1952) and other forms the toothbearing plate is, according to Jarvik, (1942), fused with the parasphenoid.

ORBITO-TEMPORAL REGION

Generally the chondrocranium of *Urodela* is but little developed and Noble (1931) attributes this fact to their slow-moving aquatic mode of life. In the orbito-temporal region the brain-case is incomplete consisting only of the two side-walls. The large dorsal opening is bounded

anteriorly by the tectum internasale and posteriorly by the tectum synoticum. The equally large ventral opening or fenestra basicranialis communis is bounded anteriorly by the planum internasale and posteriorly by the commissura hypochordalis.

A great number of urodeles have two ventral fenestra: the fenestra basicranialis anterior and the fenestra basicranialis posterior separated from each other by a cartilaginous bar, the crista sellaris (Stadtmüller, 1936). In others the crista sellaris is resorbed during ontogeny so that the adult has a large fenestra basicranialis communis. In addition to *Rhyacotriton* a fenestra basicranialis communis is characteristic of *Diemictylus*, *Plethodon* and *Pseudotriton* (Stadtmüller, 1936). In *Megalobatrachus* (Aoyama, 1930) the crista sellaris is retained, but the fenestra basicranialis posterior is filled with cartilage.

The orbitosphenoid, the only cartilage bone in the side-wall of the brain-case, extends from the antorbital cartilage to the anterior border of the foramen optico-oculomotorium (Fig. 1). The latter foramen is obviously the result of the absence of the pila metoptica and it transmits all the structures that would normally have passed through the foramen opticum and the foramen oculomotorium.

The nervus trochlearis follows an exceptional course on its way to reach the musculus obliquus superior. After running antero-laterally closely against the orbitosphenoid in a groove on its inside, it escapes from the cranial cavity through the foramen trochlearum (Fig. 7) situated in the dorsal portion of the orbitosphenoid. In *Ambystoma*

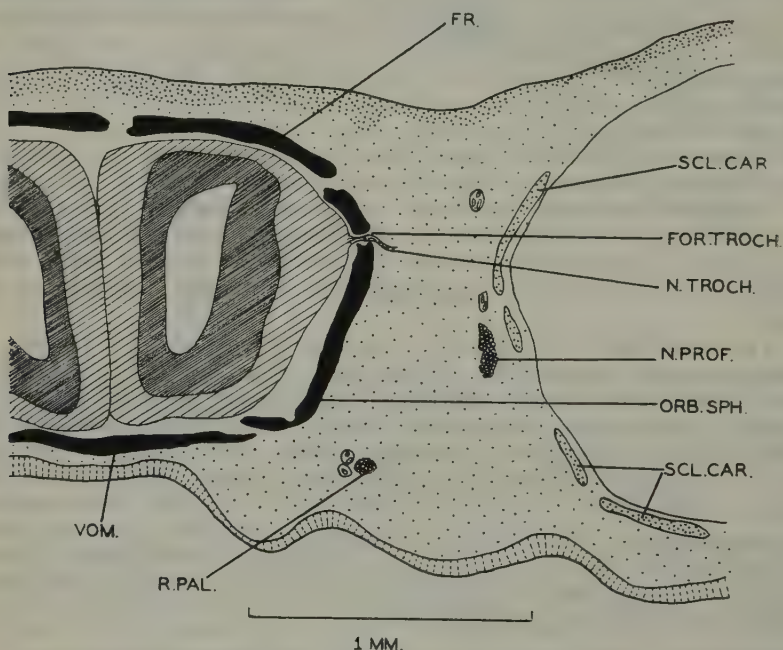


Figure 7.

Transverse section through the foramen trochleare.

FORT.TROCH., foramen trochleare; FR., frontal; N.PROF., nervus profundus; N.TROCH., nervus trochlearis; ORB.SPH., orbitosphenoid; R.PAL., ramus palatinus; SCL.CAR., sclerotic cartilage; VOM., vomer.

maculatum (Theron, 1952) the nervus trochlearis does not pierce the orbitosphenoid, but passes, as in most other urodeles, through a foramen in the parietal.

Situated behind the foramen optico-oculomotorium is the foramen prooticum which is bounded anteriorly by the pila antotica, and posteriorly by the anterior dome of the auditory capsule. The foramen prooticum accommodates the ganglion Gasseri from which emerges the nervus trigeminus. In *Ambystoma maculatum* (Theron, 1952) *Ambystoma macrodactylum* (Papendieck, 1954) and *Triturus* (Francis, 1934) the nervus abducens leaves the cranial cavity in close association with the ganglion Gasseri. In *Onychodactylus* (Ryke, 1950) and *Salamandra*

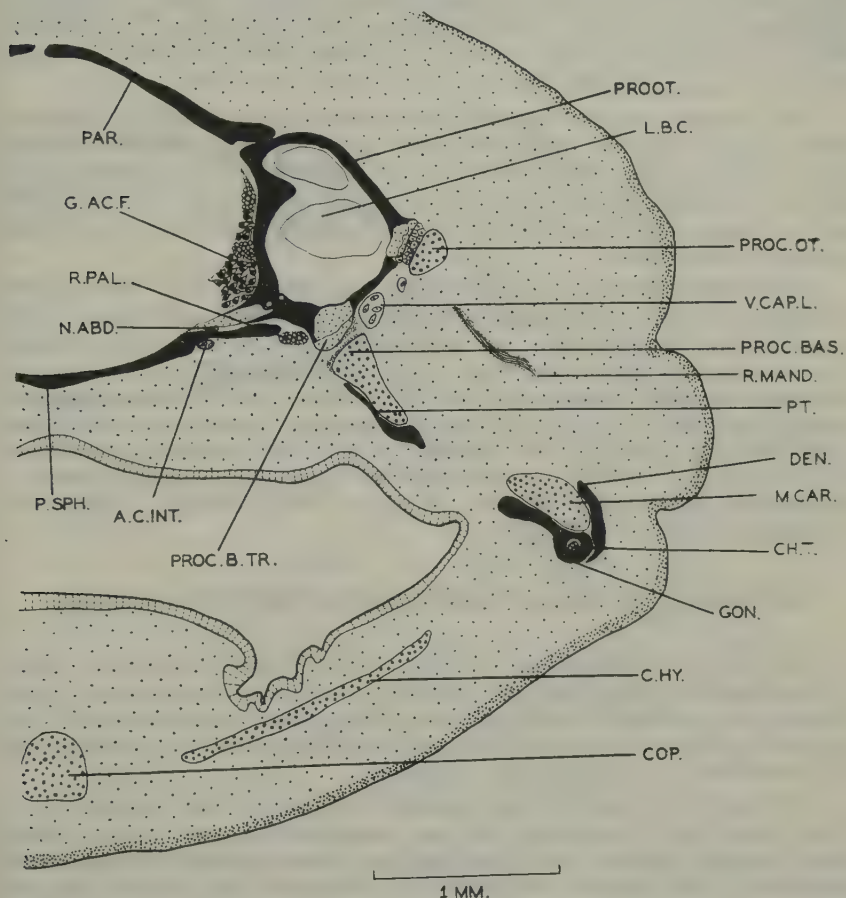


Figure 8.

Transverse section through the region of the palatobasal connexion.

A.C.INT., arteria carotis interna; CH.T., chorda tympani; C.HY., ceratohyal; COP., copula; DEN., dentary; G.A.C.F., ganglion acustico-faciale; GON., gonial; L.B.C., labyrinthine cavity; M.CAR., Meckel's cartilage; N.ABD., nervus abducens; PAR., parietal; PROC.BAS., processus basalis; PROC.B.TR., processus basitrabecularis; PROC.OT., processus oticus; PROOT., prootic; P.SPH., parasphenoid; PT., pterygoid; R.MAND., ramus mandibularis; R.PAL., ramus palatinus; V.CAP.L., vena capitis lateralis.

(Francis, 1934) the nervus abducens has its own foramen abducentis. In *Rhyacotriton* the abducent arises far posteriorly from the ventral surface of the medulla oblongata and on its way anteriorly to the orbit it runs closely along the margin of the planum basale and parallel to the ramus palatinus VII (Figs. 3 and 8). It emerges from the cranial cavity around the mesial edge of the planum basale, continues for some length between the parasphenoid and the planum basale, and supplies the mm. rectus posterior and retractor bulbi (Francis, 1934).

A special foramen in the parasphenoid transmitting the arteria carotis interna into the cranial cavity is situated mesially to the processus basalis (Fig. 2) as in *Megalobatrachus* (Aoyama, 1930). In *Salamandra* (Francis, 1934), *Onychodactylus* (Ryke, 1950), *Ambystoma maculatum* (Theron, 1952) and *Ambystoma macrodactylum* (Papendieck, 1954) the internal carotid enters the cranial cavity through a canal between the parasphenoid and the floor of the brain-case.

The sclerotic cartilage persists throughout life as a thin cartilaginous saucer-shaped capsule supporting the proximal part of the eye-ball (Fig. 7). It becomes thicker towards the centre where it is pierced by a foramen transmitting the optic nerve as well as a branch of the arteria ophthalmica. In its dorsal portion there is another small foramen transmitting a bloodvessel.

Stadtmüller (1914) suspected that the persistence of the sclerotic cartilage after metamorphosis, was a characteristic of those forms adapted to an aquatic mode of life. It is true however, that the presence of a sclerotic cartilage is indicative of primitiveness and that it becomes reduced in higher *Urodela*. In 1929 Stadtmüller modified his views by stating that there is no correlation between the degree of development of the sclerotic cartilage and the mode of life. The probable significance of the variation in size of the sclerotic cartilage in the *Urodela* is discussed by Stadtmüller (1929), De Beer (1937), Theron (1952) and Papendieck (1954).

MEMBRANE BONES OF THE ORBITO-TEMPORAL REGION

The frontal, situated over the anterior portion of the cavum cranii, is an elongated bony plate the rounded posterior extremity of which overlaps the parietal slightly. Its anterior portion lies underneath the extensive processus praenasalis of the premaxillary and antero-laterally it is overlain by the prefrontal (Fig. 1).

The parietal succeeds the frontal posteriorly and consists of a broad bony plate spreading over the posterior portion of the cavum cranii including most of the dorsal surface of the auditory capsule. Only a fraction of the tectum synoticum is left exposed. The parietal has two anteriorly directed processes of which the lateral one, termed the processus orbitalis of the parietal (Wiedersheim, 1877), bends downwards and extends further anteriorly than the median one. A shallow groove between the two prongs of the parietal accommodates the overlapping posterior extremity of the frontal. The postero-lateral part of the parietal is devoid of a supratemporal crest as in *Ambystoma macrodactylum* (Papendieck, 1954).

The parasphenoid is the largest single bone in the skull and underlies the entire floor of the brain-case. Its lateral wings spread

underneath the otic and occipital regions. Near the base of each wing is situated the carotid foramen. Its anterior tip lies dorsally to the vomers and posteriorly it extends right up to the foramen magnum (Fig. 2).

OTIC AND OCCIPITAL REGIONS

With rare exceptions only two cartilage bones, the prootic and the exoccipital, are found in the otic and occipital regions of the urodelan skull. In most urodeles they are fused into a prootico-exoccipital complex, but in *Rhyacotriton* they remain distinct. They are separated by the cartilago prootico-occipitalis (Gaupp), which together with the tectum synoticum and the commissura hypochordalis form a complete girdle. The size and relationships of these bones are best understood by referring

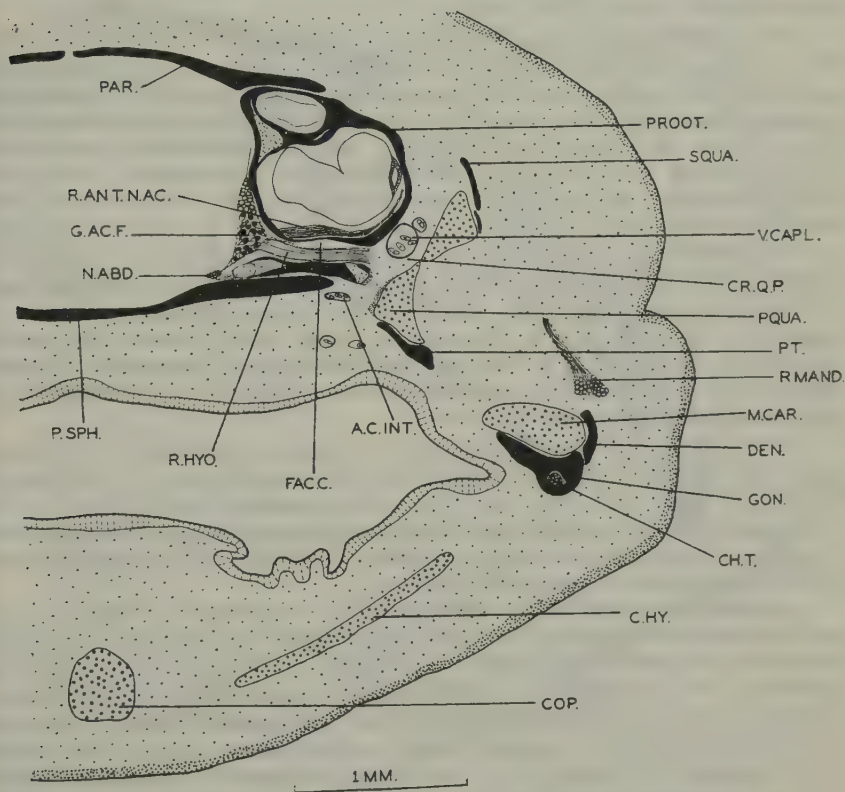


Figure 9.

Transverse section through the region of the facial canal.

A.C.INT., arteria carotis interna; CH.T., chorda tympani; C.HY., ceratohyal; COP., copula; CR.Q.P., cranioquadrate passage; DEN., dentary; FAC.C., facial canal; G.A.C.F., ganglion acustico-faciale; GON., gonial; M.CAR., Meckel's cartilage; N.ABD., nervus abducens; PAR., parietal; P.QUAD., pars quadrata; PROOT., prootic; P.SPH., parasphenoid; PT., pterygoid; R.ANT.N.AC., ramus anterior of nervus acusticus; R.HYO., ramus hyomandibularis; R.MAND., ramus mandibularis; SQUA., squamosal; V.CAP.L., vena capitis lateralis.

to figures 1 and 2. The presence of distinct prootic and exoccipital bones is regarded by Stadtmüller (1924) as a primitive feature.

All traces of the notochord have disappeared from the skull of *Rhyacotriton*. In this respect it is probably less neotenic than *Onychodactylus* (Ryke, 1950), *Ambystoma macrodactylum* (Papendieck, 1954) and *Ambystoma maculatum* (Theron, 1952) in which vestiges of the notochord are found in the skull.

The antero-dorsal part of the squamosal overlaps the rounded edge of the dorso-lateral side of the prootic (Fig. 12). In *Ambystoma macrodactylum*, *A. gracile* and *A. maculatum* (Eaton, 1933; De Villiers, 1936; Theron, 1952; Papendieck, 1954) the prootic has a crest-like process which overhangs the squamosal. According to Eaton (1933) this process probably serves as a fulcrum for the movement of the squamosal. In *Rhyacotriton* the squamosal overlaps the smooth lateral part of the prootic and it is possible that some gliding movement may take place between them (De Villiers, 1936).

The medial wall of the otic capsule is pierced by certain foramina. The recessus acustico-facialis is an extensive recess in the ventro-lateral region of the ganglion acustico-faciale. Communication with the ganglion Gasseri is established by means of an intracranial ramus communicans (Fig. 3), as in *Salamandra* (Francis, 1934), *Ambystoma maculatum* (Theron, 1952) and *Ambystoma macrodactylum* (Papendieck, 1954). The ramus palatinus of the facial nerve after emerging from the ganglion acustico-faciale continues antero-ventrally, piercing the base of the skull at the foramen palatinum. The ramus hyomandibularis, intimately associated with the extracranial ramus communicans, passes through the facial canal, and upon entering the cranioquadrate passage, it separates from the ramus communicans and turns towards the medial margin of the lower jaw. The extracranial ramus communicans forms the connexion between the ganglion acustico-faciale and the ganglion of the glossopharyngeal-vagus nerves.

The ramus hyomandibularis and r. palatinus emerge very clearly from the cranial cavity through the facial canal and are completely separated from the otic cavity by the capsular wall (Fig. 9). In *Triturus* where the medial wall of the facial canal remains cartilaginous it appears that the facial nerve emerges from the otic cavity. De Beer (1937) considers it a primitive feature.

Leaving the ganglion acustico-faciale, the ramus anterior of the nervus acusticus enters the otic capsule through the foramen acusticum anterius, situated in the medial wall exactly above the facial canal. The capsular wall separates the ramus anterior from the ramus hyomandibularis. The ramus medianus enters the otic capsule further back with its foramen situated ventrally in the cartilaginous part of the medial wall. Immediately behind it is the larger foramen acusticum posterius for the ramus posterior. The two foramina are separated by a very thin cartilaginous strip. This pattern is repeated on both sides of the specimen examined although in other species the number of foramina is subject to variation (Papendieck, 1954), (Theron, 1952).

The foramen endolymphaticum is situated dorsally to the foramen acusticum posterius and the position of the foramen perilymphaticum is further back in the ventral part of the medial wall between the cartilago prootico-occipitalis and the bony exoccipital. Finally, situated in the exoccipital immediately posterior to the otic capsule is the foramen postoticum (for. metoticum, Stadtmüller, 1936) for the transmission

of the glossopharyngeal-vagus nerves. It opens to the exterior laterally to the condylus occipitalis (Fig. 2). It may be noted that the glossopharyngeal-vagus ganglion has an extracranial position as indicated in the scheme of the cranial nerves.

THE COLUMELLA AURIS

In the *Ambystomidae* the sound-conducting apparatus consists typically of two separate elements, the operculum and the columella, and according to Dunn (1922) *Rhyacotriton* conformed to the typical ambystomid condition. In 1938, however, De Villiers showed that *Rhyacotriton* lacked an operculum, an observation which was confirmed by Dunn (1941). Since the fenestra ovalis is situated in the cartilago prootico-occipitalis its border consists of cartilage.

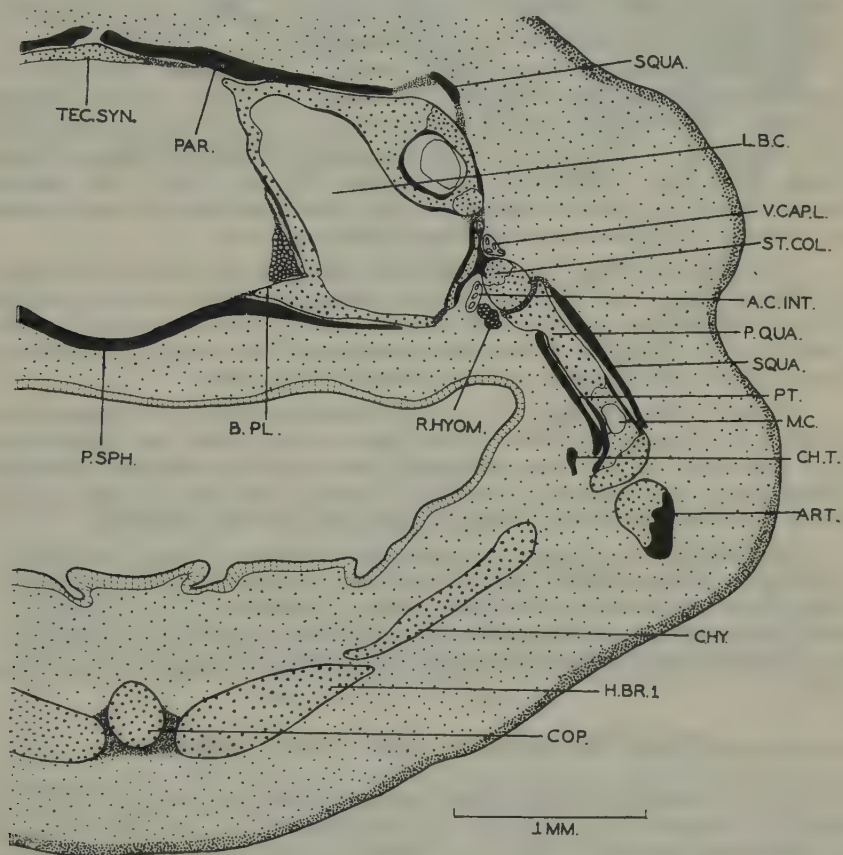


Figure 10.

Transverse section through the stylus columellae.

A.C.INT., arteria carotis interna; ART., articular; B.PL., basal plate; CH.T., chorda tympani; C.HY., ceratohyal; COP., copula; H.BR. I, hypobranchial 1; L.B.C., labyrinthine cavity; M.C., marrow cavity; PAR., parietal; P.QUA., pars quadrata; P.SPH., parasphenoid; PT., pterygoid; R.HYOM., ramus hyomandibularis; SQUA., squamosal; ST.COL., stylus columellae; TEC.SYN., tectum synoticum; V.CAP.L., vena capitis lateralis.

The columella consists of a medially flattened footplate and a laterally projecting stylus columellae (Fig. 10). The footplate occupies the larger portion of the fenestra ovalis. Its posterior part is syndesmotically joined to the margin of the fenestra, but its anterior part is confluent with the cartilaginous wall of the fenestra. The footplate is perichondrally ossified on both its inner and outer surfaces, the ossification of the latter extending into the stylus columellae (Fig. 10). According to Kingsbury and Reed (1909) this method of ossification of the columella is characteristic of other urodeles as well. The margin of the footplate, however, remains cartilaginous. The distal end of the stylus columellae which merges into the pars quadrata of the palatoquadrata is massively cartilaginous. The columella auris is a solid structure, lacking a marrow cavity. In forms like *Hynobius* (De Villiers, 1938), *Ambystoma maculatum* (Theron, 1952) and *Ambystoma macrodactylum* (Papendieck, 1954) it possesses a marrow cavity; hence its flimsy structure in *Ambystoma maculatum* (Theron, 1952).

As in *Onychodactylus* (Ryke, 1950) the stylus columellae is synchondrotically connected to the pars quadrata palatoquadrati, resulting in the replacement of the ligamentum suspensorio-columellare. This ligament is well developed in *Ambystoma macrodactylum* (Papendieck, 1954) and *Ambystoma maculatum* (Theron, 1952). The suspensorial attachment to the columella shows great variation in the *Urodela*, as indicated by Kingsbury and Reed (1909).

The relation of the bloodvessels and nerves to the stylus columellae is typical. The vena capitis lateralis passes dorsally over the stylus, the arteria petrosa lateralis and arteria carotis interna pursue a course ventral to the stylus and the three branches of the ramus hyomandibularis VII emerge ventrally to the columella (Fig. 10).

Owing to the absence of the operculum the musculus opercularis is lacking and the conduction of sound waves to the inner ear must therefore take place in a manner different from that in other ambystomids. Sound waves are probably conducted through the floor of the mouth, lower jaw, suspensorium, columella and finally to the inner ear.

An operculum is present in *Salamandra* (Francis, 1934), *Ambystoma maculatum* (Theron, 1952) and *Ambystoma macrodactylum* (Papendieck, 1954), to mention only a few. The unique condition of a fused columella and operculum in the *Plethodontidae* and *Desmognathidae* is regarded as a characteristic feature of these two families (Kingsbury and Reed, 1909).

PALATOQUADRATA AND SUSPENSORIUM

The two major divisions of the palatoquadrata are the pars quadrata and the pars palatina. The latter is represented by a slender rod, the processus pterygoideus (Fig. 1), directed anteriorly and terminating medially to the processus maxillaris posterior.

The pars quadrata is the larger portion of the palatoquadrata and bears three processes directed towards the neurocranium. The cranioquadrata passage (Goodrich, 1931) is enclosed between the pars quadrata, its processes, and the chondrocranium (Fig. 9). Passing through the cranio-quadrata passage is the ramus jugularis VII — the ramus communicans (Fig. 3) accompanied by the vena capitis lateralis and the closely associated arteria petrosa lateralis. Similar conditions

obtain in *Salamandra* (Francis, 1934), but in *Ambystoma macrodactylum* (Papendieck, 1954) and *Ambystoma maculatum* (Theron, 1952) the a. petrosa lateralis runs ventral to the passage.

The processus ascendens is a slender cartilaginous rod projecting from the foremost part of the pars quadrata in a dorsal direction where it finds a synchondrotic connexion with the pila antotica (Figs. 2 and 11).

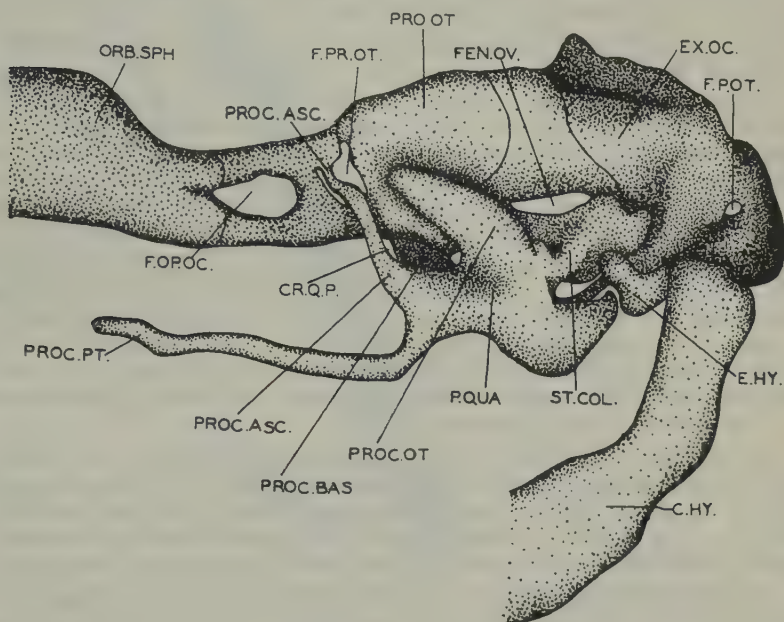


Figure 11.

Graphic reconstruction of palatoquadrate and suspensorium x approx. 22.2. Lateral view.

C.HY., ceratohyal; CR.Q.P., cranioquadrate passage; E.HY., epihyal; EX.OC., exoccipital; FEN.OV., fenestra ovalis; F.OP.OC., foramen optico-oculomotorium; F.P.OT., foramen postoticum; F.PR.OT., foramen prooticum; ORB.SPH., orbitosphenoid; P.QUA., pars quadrata; PROC.ASC., processus ascendens; PROC.BAS., processus basalis; PROC.OT., processus oticus; PROC.PT., processus pterygoideus; PROOT., prootic; ST.COL., stylus columellae.

Anteriorly the processus ascendens separates the ramus ophthalmicus profundus from the ramus maxillaris V and ramus mandibularis V and lies in a position dorso-lateral to the vena capitis lateralis and a branch of the arteria carotis interna. The relationships of the processus ascendens to neighbouring structures are more or less similar to those in *Ambystoma maculatum* (Theron, 1952), *Rhyacotriton* (De Villiers, 1938), *Ambystoma macrodactylum* (Papendieck, 1954) and *Onychodactylus* (Ryke, 1950). The processus ascendens undergoes perichondral ossification in *Salamandra* (Francis, 1934).

The processus oticus is synchondrotically attached to the crista parotica on the dorso-lateral surface of the otic capsule (Fig. 8). The strongly developed process is situated behind the branches of the trigeminal nerve and in front of the facial nerve, and its point of

attachment to the crista parotica is vertically above the processus basalis. It agrees in all essentials with that of *Ambystoma maculatum* (Theron, 1952), *Ambystoma macrodactylum* (Papendieck, 1954) and *Onychodactylus* (Ryke, 1950). In the juvenile specimen described by De Villiers (1938) the otic process is still undeveloped.

The processus basalis is a relatively broad cartilaginous structure reaching the base of the skull where a diarthrotic connexion is formed with the processus basitrabecularis (Figs. 8 and 11). The process lies ventrally to the vena capitis lateralis and to the ramus hyomandibularis VII and it forms the ventral boundary of the cranio-quadrate passage. The ramus palatinus VII is situated medially to it. The slightly irregular articular surfaces of the diarthrotic palatobasal connexion may possibly allow a somewhat restricted rotatory movement of the palatoquadrate. Stadtmüller (1936) remarks that similar diarthrotic connexions obtain in *Plethodon*, *Hynobius* and *Chioglossa*, to which may be added *Ambystoma maculatum* (Theron, 1952) and *Ambystoma macrodactylum* (Papendieck, 1954). This condition is regarded by Gaupp (Stadtmüller, 1936) as primitive. In *Onychodactylus* (Ryke, 1950) the palatobasal diarthroses are different, not only in the various specimens examined but also on the two sides of the same skull. In the specimen described by Stadtmüller (1936) there is a diarthrosis on the one side, whereas the other side shows the synchondrotic palatobasal connexion characteristic of the majority of the urodeles.

An epihyal occurs as a cartilaginous structure with its proximal end in syndesmosis with the extreme posterior end of the pars quadrata, whereas its distal end is fused with the dorsal tip of the ceratohyal (Fig. 11). The identity of the epihyal is established by its fibro-cartilaginous nature, whereas the ceratohyal consists of hyaline cartilage.

The circumstance that, in this particular specimen of *Rhyacotriton olympicus* the epihyal effects a syndesmotic union with the pars quadrata, means that its jaw suspension is of the amphistylic type. However, there seems to be great variation in this region of the ambystomid skull. Eaton (1933) found an epihyal in *Ambystoma macrodactylum*, *Ambystoma gracile* and in *Rhyacotriton*. In the specimen of *Ambystoma macrodactylum* described by De Villiers (1938) there is an epihyal only on the one side, whereas in Papendieck's specimens no such element could be found. It is also lacking in *Ambystoma maculatum* (Theron, 1952) as well as in the juvenile specimen of *Rhyacotriton* described by De Villiers in 1938 and in *Salamandra* (Francis, 1934). According to the available evidence a ligamentum hyoquadratum stretches between the pars quadrata and the ceratohyal in all the forms lacking an epihyal.

As mentioned before the stylus columellae is synchondrotically fused with the postero-medial side of the pars quadrata (Fig. 11).

Above the articular region the pars quadrata becomes enchondrally ossified to form the quadrate (Fig. 12).

The quadratojugal is a membrane bone on the anterior outer surface of the pars quadrata palatoquadrati. The separating connective tissue between the lower region of this membrane bone and the quadrate disappears. A mixed bone is formed: quadratojugal simulating perichondral ossification of the quadrate (Fig. 12).

The squamosal is a membrane bone of the dorso-lateral part of the suspensorium and it also extends over the lateral aspect of the otic

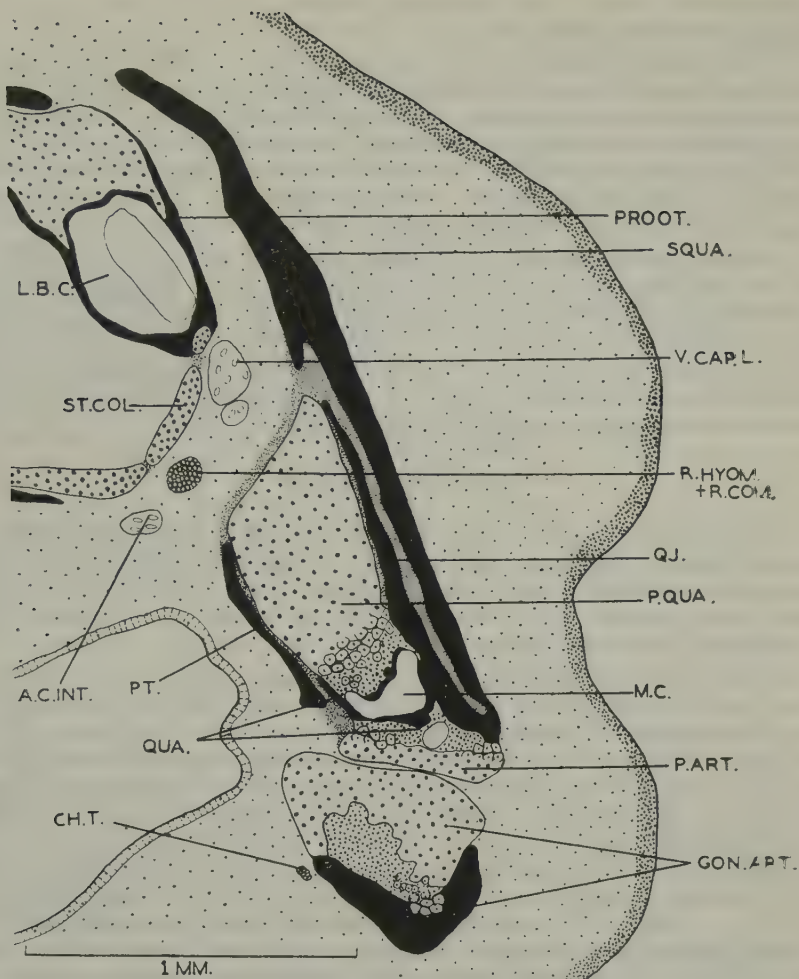


Figure 12.

Transverse section showing invasion of the quadrate region by the quadrato-jugal.

A.C.INT., arteria carotis interna; CH.T., chorda tympani; GON.ART., gonioarticular; L.B.C., labyrinthine cavity; M.C., marrow cavity; P.ART., pars articularis; P.QUA., pars quadrata; PROOT., prootic; PT., pterygoid; Q.J., quadrato-jugal; QUA., quadrate; R.HYOM. + R.COM., ramus hyomandibularis + ramus communicans; SQUA., squamosal; ST.COL., stylus columellae; V.CAP.L., vena capitis lateralis.

capsule. The lower part of the squamosal covers almost the entire quadratojugal, only the extreme ventral tip of the latter being visible from the outside.

A zygomatic process is absent as in most urodeles. In species in which it does occur, such as *Ambystoma maculatum* (Theron, 1952), it probably represents a vestige of the upper temporal arcade (De Villiers, 1936). The fact that the lower tip of the squamosal is fused with the

quadratojugal over a short distance, renders relative movement of these bones impossible (Fig. 12).

The general shape of the pterygoid can be best understood by referring to text-figure 2 in which it is featured in ventral view. Close to the pars quadrata the anterior horizontal lamina of the pterygoid almost envelopes the processus pterygoideus. It invests the basal process ventrally and then extends into the vertical lamina applied to the medial surface of the pars quadrata. It reaches back into the articular region where its lower part overlaps the quadrata (Figs. 2, 8 and 12).

Eaton (1933) considered *Rhyacotriton* and the other ambystomids to be streptostylic and maintained that the pars quadrata and the associated squamosal had a pivotal action on the otic capsule. However, since subsequent accounts by De Villiers (1936, 1938), Theron (1952) and Papendieck (1954) have shown that both the ascending and the otic processes are fused with the neurocranium, the skull of the ambystomids is most probably monimostylic.

THE LOWER JAW

The structure of the lower jaw conforms to the general pattern in *Ambystomidae*. Meckel's cartilage is retained throughout life as a slender rod which gradually becomes thicker towards the back. The distal ends bend inwards and fuse intimately by means of a cartilaginous connexion, the mental symphysis.

Ossification of Meckel's cartilage takes place in two regions resulting in the formation of two cartilage bones, the mentomandibular and the articular. The mentomandibular appears at the distal end of Meckel's cartilage and is fused with the dentary. Similar conditions are found in *Ambystoma maculatum* (Theron, 1952), *Ambystoma macrodactylum* (Papendieck, 1954), *Megalobatrachus* (Aoyama, 1930), *Onychodactylus japonicus* (Ryke, 1950; Okajima, 1908) as well as in several *Salamandridae* studied by Stadtmüller (1936). Papendieck (1954) mentions the occurrence of a marrow cavity in the mentomandibular-dentary complex in *Ambystoma macrodactylum*. Investigations on *Rhyacotriton* and *Ambystoma maculatum* (Theron, 1952) fail to show the presence of a marrow cavity. The cartilaginous substance situated in the centre portion along the mentomandibular-dentary complex is in various stages of enchondral ossification and this condition only simulates a marrow cavity.

In the articular region Meckel's cartilage ossifies as the articular. In *Megalobatrachus* (Gaupp, 1911) and *Necturus maculatus* (Stadtmüller, 1936) the pars articularis remains unossified, resulting in the absence of the articular. In some forms, including *Salamandra maculosa*, *S. atra* and *Ambystoma tigrinum* (Stadtmüller, 1936), the articular is unattached to any membrane bone. In the majority of urodeles, however, the articular fuses with the gonial. A gonio-articular is found in most ambystomids, in *Megalobatrachus* (Aoyama, 1930), *Triturus* and in the majority of *Salamandridae* (Stadtmüller, 1924). An additional fusion of the gonio-articular with the dentary may take place to form a dento-gonio-articular, occurring in *Ambystoma opacum* and *Ambystoma microstomum* (Stadtmüller, 1936).

Meckel's cartilage is situated in the canalis primordialialis, formed by the dentary on the outside and the gonial on the inside. Bloodvessels

and branches of the fifth and seventh nerves also pass through the canalis primordialialis.

The dentary is the largest membrane bone in the lower jaw, and extends from the mentomandibular to the articular region. Furthermore, the paired dentaries are the only toothbearing bones of the lower jaw. There is a single row of monocuspid, pleurodont teeth restricted to the anterior half of the bone. Isolated teeth anlagen are found along the inside of the dentary teeth. The dentary, for some distance completely encircles the anterior part of Meckel's cartilage, but proximally it becomes restricted to the ventro-lateral side of the cartilage as in *Ambystoma maculatum* (Theron, 1952), *A. macrodactylum* (Papendieck, 1954) and several other species described by Stadtmüller (1936).

The only nerve branches situated in the canalis primordialialis are the ramus mandibularis internus V and the ramus alveolaris VII. Both these branches extend anteriorly and upon leaving the canalis primordialialis between the dorsal edges of the dentary, split into fine twigs which supply the teeth and the floor of the buccal cavity.

The course of the ramus mandibularis externus differs widely from that in *Salamandra maculosa* described by Stadtmüller (1924). The ramus mandibularis externus runs forwards completely external to the canalis primordialialis, but closely applied to the lateral face of the dentary. It breaks up into fine twigs supplying the skin overlying the lower jaw.

The courses of these nerves account for the absence of the foramina dento-facialia. The latter do however occur in *Ambystoma macrodactylum* (Papendieck, 1954) and in *Ambystoma maculatum* (Theron, 1952).

The gonial is an investing bone of the medial, proximal part of Meckel's cartilage. It fuses with the articular to form the gonio-articular (Fig. 12). Immediately in front of the articular region it increases in height to form the coronoid process. Furthermore, the gonial is pierced by the canalis alveolaris. Stadtmüller (1936) states that in some *Perrennibranchiata* the ramus alveolaris does not perforate the gonial but remains medial to it. Hentschel (1936) mentions that there is no canalis chordae tympani in *Siren lacertina*.

Beyond the articular region Meckel's cartilage projects as a post-articular process for the insertion of the musculus depressor mandibulae.

THE HYOBANCHIAL APPARATUS

After metamorphosis the hyobranchial apparatus is concerned with the air-breathing function and the movement of the tongue. The hyobranchial skeleton consists of a complete hyoid arch and two branchial arches.

The hyoid arch consists of the epihyal, the ceratohyal and the hypohyal, the latter being represented by the radius anterior (Fig. 13). Each radius anterior forms a synchondrotic connexion with the copula. The diverging anterior ends of the radii anteriores are embedded in the firm tissue of the tongue. The radius anterior has lost its attachment to the ceratohyal as in *Salamandra maculosa* (Gaupp, 1905). In *Ambystoma maculatum* (Theron, 1952) and *A. macrodactylum* (Papendieck, 1954) a strong ligament stretches between the radius anterior and the ceratohyal. In *Triturus* and in *Pseudotriton* the hypohyal is absent (Gaupp, 1905). In the Asiatic salamanders *Megalobatrachus* (Aoyama, 1930) and *Onychodactylus* (Fukuda, 1930) the hypohyal is

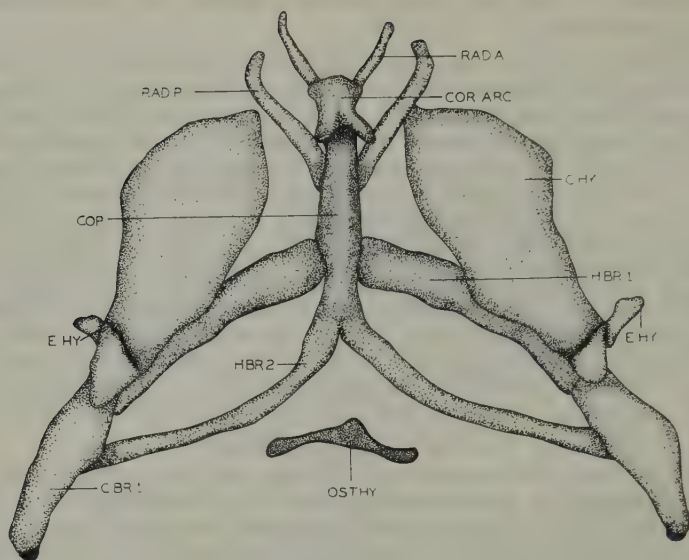


Figure 13

Dorsal view of the hyobranchial apparatus x approx. 14.8.

C.BR. 1, ceratobranchial 1; C.HY., ceratohyal; COP., copula; COR.ARC., corpus arcuata; E.HY., epihyal; H.BR. 1, hypobranchial 1; H.BR. 2, hypobranchial 2; OS.THY., os thyroideum; RAD.A., radius anterior; RAD.P., radius posterior.

fused with the ceratohyal. Fox (1959) gives a detailed account of the ontogeny of the hyobranchial apparatus in five larval stages of *Hynobius nebulosus* and also reviews the literature on the subject.

The tapering proximal end of the ceratohyal curves upwards to the suspensorial region. It is confluent with the epihyal, but as previously mentioned, the identity of the two elements is manifested by the difference in their histological structure.

The paired radii posteriores are horn-like structures which are in synchondrotic connexion with the ventral face of the copula. In *Pseudotriton* the radii posteriores are absent (Gaupp, 1905).

The cartilago arcuata may be defined as an uninterrupted arch (Wiedersheim, 1877) dorsal to the copula forming the union between the radii posteriores. In *Rhyacotriton*, however, a cartilaginous saddle-shaped structure, situated medially and dorsally over the anterior tip of the copula, apparently represents the cartilago arcuata (Fig. 13), two posteriorly directed processes are in weak syndesmotic connexion with the radius posterior of either side. These blunt processes evidently represent the remains of a rodlike cartilago arcuata as found in *Ambystoma maculatum* (Theron, 1952), *Ambystoma macrodactylum* (Papendieck, 1954) and *Triturus* (Gaupp, 1905). The broad anterior part of the corpus arcuata is syndesmotically connected with the radii anteriores some distance in front of their union with each other.

The only remaining elements of the first and second branchial arches are the hypobranchial I, ceratobranchial I and hypobranchial II (Fig. 13). The hypobranchials II are fused with the copula, but the lines of fusion are histologically clearly discernible.

The copula is the median body to which the elements of the hyobranchial skeleton are attached. The greater part of the larval copula stalk is resorbed during metamorphosis; its hindmost part, however, persists and becomes ossified as the os thyroideum containing a central marrow cavity.

SUMMARY

- 1 The fenestra praecerebralis is present.
- 2 The fenestra retronarina occurs far back and is situated in the planum conchale; it transmits the ramus lateralis nasi and no longer houses the lateral diverticulum of the nasal sac.
- 3 The fenestra retronarina is not confluent with the incisura ectochoanalis.
- 4 The cavum internasale is large and separates the two nasal capsules; it thus replaces the septum internasale functionally.
- 5 The processus praenasalis superior medius is entirely absent.
- 6 Seydel's "palatal process" cannot be recognized as a free posteriorly projecting process.
- 7 The lacrimal on the right side is fused posteriorly with the prefrontal, but the left one remains independent. Both contain a large canal for the ductus nasolacimalis, which also pierces the septomaxillary.
- 8 The vomerine teeth are arranged in two short arched rows and are restricted to the postero-medial area of the bone.
- 9 There is no separate palatine.
- 10 The cartilago prootico-occipitalis is an extensive girdle-shaped strip around the centre of the otic capsule.
- 11 The crista sellaris and all traces of the intracranial portion of the notochord are absent.
- 12 There are three foramina acustica on either side.
- 13 The sound-conducting apparatus consists of a single element, the stylus columellae, the footplate of which is confluent with the anterior wall of the fenestra ovalis.
- 14 The stylus columellae is synchondrotically connected to the pars quadrata palatoquadrati, the ligamentum suspensorio-columellare being absent.
- 15 The operculum and the musculus opercularis are absent.
- 16 The processus ascendens palatoquadrati is synchondrotically fused with the pila antotica.
- 17 The processus oticus is connected to the crista parotica by means of a synchondrosis.
- 18 A diarthrotic connexion occurs between the processus basalis and the processus basitrabecularis.
- 19 The quadratojugal is indistinguishably fused to the quadrate.
- 20 The zygomatic process of the squamosal is absent.
- 21 The dentary is not perforated by foramina dento-facialia.

- 22 The ramus mandibularis externus runs along the lateral side of the dentary. Anteriorly it is completely excluded from the canalis primordialialis.
- 23 There is no narrow cavity in the mentomandibular-dentary complex.
- 24 The articular is fused with the gonial.
- 25 An epihyal may be distinguished and there is no ligamentum hyoquadratum.
- 26 The ceratohyal has lost its connexion with the hypohyal.
- 27 The os thyreoideum contains a marrow cavity.

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THE CRANIAL ANATOMY AND KINESIS
OF THE BIRD SNAKE
THELOTORNIS CAPENSIS (SMITH)

by

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(With 12 text-figures)

Thesis accepted for the Master's Degree in Zoology
at the University of Stellenbosch

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ABSTRACT

The chondrocranium and the osteocranium of a late developmental stage of *Thelotornis* are described and compared with those of other snakes. Great similarity was found with *Tropidonotus* as described by Bäckström (1931). The mutual relations of the different bony elements and the trigeminus muscles were investigated in connexion with kinesis. A possible connexion between the m. retractor vomeris and the functioning of the organ of Jacobson is postulated.

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INTRODUCTION

The genus *Thelotornis* belongs to the subfamily *Boiginae* and is confined to the Ethiopian region.

In 1844 Hallowell described a snake which he named *Leptophis kirtlandii*. This snake came from West Africa (Liberia). In 1849, however, Smith described the Southern form as *Thelotornis capensis*. Since then it has also been described under various other generic names such as *Cladophis*, *Oxybeles*, *Dryiophis* and *Tragops*. Until 1940 the genus was regarded as monotypic. In that year Bogert carried out a re-investigation of this genus and explained the external morphological and colour differences as correlated with habitat. *Thelotornis kirtlandii* is confined to the limits of the rain forests, ranging from Portuguese Guinea to northern Angola, east to southern Somaliland and central Tanganyika Territory. *Thelotornis capensis*, on the contrary, is found only in the savannah of central Angola, northern South West Africa, eastern to central Tanganyika Territory and Natal (Loveridge, 1944).

MATERIAL AND TECHNIQUE

I am much indebted to Dr. J. Pringle of the Natal Museum, for supplying me with a complete series of embryos of *Thelotornis capensis*.

An 86 day old embryo (9 cm.) and a newly hatched 131 day old specimen (14.9 cm.) were used for this investigation. The snakes were obtained from Nelspruit in the Transvaal, and a batch of eggs was incubated at the Port Elizabeth snake park.

The embryos were fixed in Bouin's solution and preserved in 70% alcohol. They were decalcified in a 6% solution of concentrated nitric acid in 70% alcohol. After decalcification the excess acid was removed by washing the specimens in a 5% solution of Na_2SO_3 . Xylol was employed as a clearing agent, and the specimens were subsequently embedded in paraffin wax (M.P. 50-52°C). The sections were stained with azocarmine and counterstained with azan, according to Romeis (1948). Graphic reconstructions were made of the skull and nasal capsule.

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THE CARTILAGINOUS NASAL CAPSULE

The description of the nasal capsule is based on the 131 day stage. Important differences between it and the 86 day stage are noted.

The cartilaginous nasal capsules are fused to the nasal septum over almost half their length. The nasal septum, triangular in cross-section, flattens towards its anterior end, where it terminates and fits into a groove in the premaxillary (Fig. 5). The greater part of the nasal septum lies in a bony canal bordered by the nasals dorsally, septomaxillary laterally and vomers ventrally (Fig. 4).

The dome-shaped cupola anterior forms the anterior wall of the nasal capsule. A large fenestra narina for the external nasal aperture is situated in the side-wall of the capsule. The processus alaris inferior projects posteriorly from the anterior cupola and forms part of the

ventral boundary of the fenestra. Behind the fenestra, the dorso-lateral edge of the side-wall curves round ventrally to form a processus alaris superior (Fig. 2). A small piece of cartilage lies ventrally to the processus alaris superior and is apparently a detached part of the processus alaris inferior (Figs. 1 and 2). In the 86 day stage it is not yet present.

Halfway along the length of the paries nasi, the conchal fold commences as a shallow groove, the so-called sulcus terminalis. As the side-wall encroaches more deeply upon the nasal cavity, the sulcus narrows and deepens to form a u-shaped concha nasalis, the hind part of which forms a blind empty pocket with incomplete walls (Fig. 1). Owing to the poor development of the side-wall, the concha is visible from the side (Fig. 2). There is no extrachonchal process as in *Hemachatus* (Pringle, 1954) and *Leptodeira* (Brock, 1929). A bony process extending medially from the ventral edge of the prefrontal partly penetrates the lateral wall of the hind part of the concha nasalis. Pringle (1954) found a similar structure in *Dasypeltis* and *Hemachatus* and regards it as a support for the concha nasalis. The glandula nasalis lateralis overlies the side-wall of the nasal capsule from the region of the processus alaris superior and extends backwards into the lumen

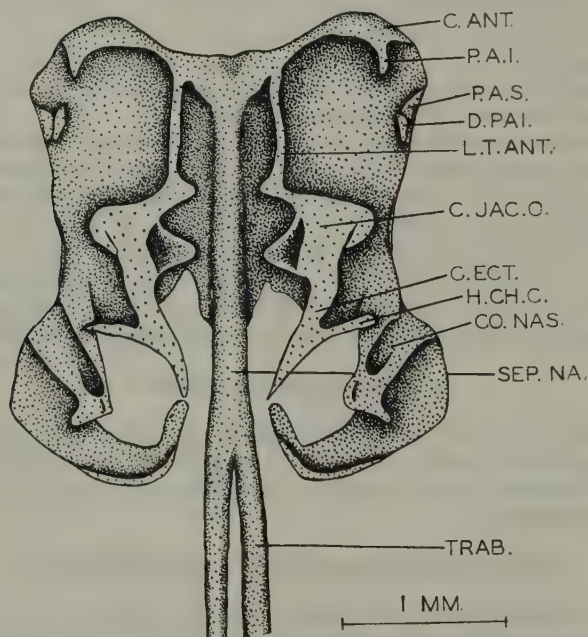


Figure 1.

Graphical reconstruction of the ventral aspect of the cartilaginous nasal capsule of the 131 day stage of *Thelotornis capensis*

C.ANT., cupola anterior; C.ECT., cartilago ectochoanalis; C.JAC.O., cartilage of Jacobson's organ; CO.NAS., concha nasalis; D.PAI., detached portion of the processus alaris inferior; H.CH.C., hypochoanal cartilage; L.T.ANT., lamina transversalis anterior; P.A.I., processus alaris inferior; P.A.S., processus alaris superior; SEP.NA., septum nasi; TRAB., trabecula.

of the front part of the concha nasalis. Posteriorly the gland lies ventrally to the floor of the blind pocket. The duct of the gland opens dorso-posteriorly into the nasal tube.

The floor of the nasal capsule is reduced anteriorly to a slender rod of cartilage, the lamina transversalis anterior, which reaches from the medio-ventral edge of the anterior cupola to the cartilage of Jacobson's organ. The cartilage of Jacobson's organ consists of a large dorsally concave floor with a concha on its medial edge; the latter structure protrudes through a fissure on the lateral surface of the vomer (Fig. 6 and 4). The floor of the capsule is very similar to that of *Tropidonotus* (Bäckström, 1931). Bäckström, however, calls the slender rod of cartilage, connecting the cupola to the cartilage of Jacobson's organ, a cartilago paraseptalis anterior. In *Lamprophis* and *Hemachatus* (Pringle, 1954) the lamina transversalis anterior is represented by an elongated process projecting posteriorly from the ventral surface of the anterior cupola but it does not reach the cartilage of Jacobson's organ. Immediately in front of the cartilage of Jacobson's organ, in *Thelotornis*, a process projects dorso-medially from the lamina transversalis anterior in the direction of the nasal septum but does not fuse with it (Figs. 1 and 2). This process is wedged in syndesmotically between the ventral surface of the septomaxillary and the anterior projection of the vomer.

Broman (1919) has described the possible mode of functioning of the organ of Jacobson in reptiles: pressure applied to the palate immediately lateral and behind the opening of the organ of Jacobson

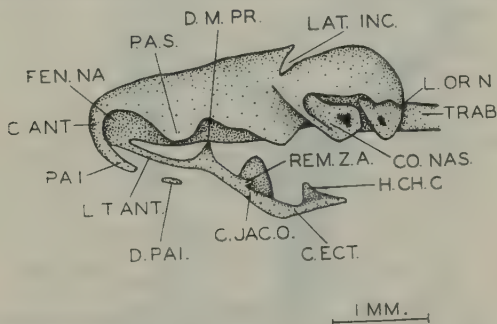


Figure 2.

Graphical reconstruction of the lateral aspect of the cartilaginous nasal capsule of the 131 day stage of *Thelotornis capensis*

C.ANT., cupola anterior; C.ECT., cartilago ectochoanalis; C.JAC.O., cartilage of Jacobson's organ; CO.NAS., concha nasalis; D.M.PR., dorso medial projection of lamina transversalis anterior; D.PAL., detached portion of the processus alaris inferior; FEN.NA., fenestra narina; H.CH.C., hypochoanal cartilage; LAT.INC., lateral incisura (remnant of the foramen epiphaniale); L.OR.N., lamina orbitonasalis; L.T.ANT., lamina transversalis anterior; P.A. I., processus alaris inferior; P.A.S., processus alaris superior; REM.Z.A., remnant of the zona annularis; TRAB., trabecula.

pushes the concha of the cartilage of Jacobson's organ upwards against the wall of the organ. Decrease of pressure results in a suction action of the organ. Haas (1930) describes in the *Glauconiidae* a muscle, the m. retractor vomeris, originating from the skull base and inserting onto the dorso-posterior edge of the vomer. The muscle is also found in *Thelotornis* and seems to be merely a separate slip of the kinetic muscle, the m. retractor pterygoidei (see also page 171). It seems highly likely that the contraction of this muscle slip could also be concerned in the emptying of the organ of Jacobson. Any active movement of the vomer should cause movement of the cartilage of Jacobson's organ and therefore exert pressure on the organ itself.

The cartilago ectochoanalis projects posteriorly from the cartilage of Jacobson's organ and is continuous with the laterally projecting rod, the hypochoanal cartilage. De Beer (1937) considers it possible that this latter cartilage represents the processus maxillaris posterior which is possibly a remnant of the ethmoid process of the palatoquadrate.

The ductus nasolacrimalis passes through the foramen nasolacrimalis in the antero-ventral surface of the prefrontal, and extends anteriorly, lateral to the choanal passage. In the region of the hypochoanal cartilage it suddenly acquires a ventro-medial position, continuing anteriorly in the space between the ectochoanal cartilage and the vomer. The ductus nasolacrimalis opens laterally into the duct of Jacobson's organ. "Snakes, therefore, resemble the *Xantusiidae* and *Amphisbaenidae* in as much as their duct does not actually open into the choana" (Malan, 1946). According to the same author the anterior

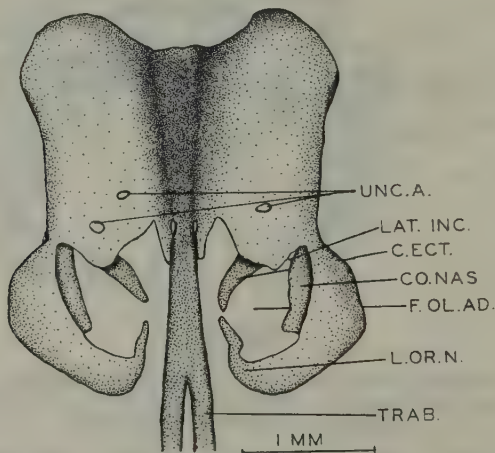


Figure 3.

Graphical reconstruction of the dorsal aspect of the cartilaginous nasal capsule of the 131 day stage of *Thelotornis capensis*

C.ECT., cartilago ectochoanalis; CO.NAS., concha nasalis; F.OL.AD., fenestra olfactoria advehens; LAT., INC., lateral incisura (remnant of the foramen epiphaniale); L.OR.N., lamina orbitonasalis; TRAB., trabecula; UNC.A., uncondrified areas.

palatal end of the ductus nasolacrimalis lying in front of the choana "is homologous with a choanal groove, transformed into a duct by the presence of both upper and the lower 'secondary palates' of Fuchs" (op. cit., p. 131).

Immediately in front of the lateral conchal fold the paries nasi forms a slight ventral projection, while the lateral edge of the cartilage of Jacobson's organ extends dorso-laterally towards it (Fig. 2 and 4). These could be considered as remnants of the zona annularis as described for *Tropidonotus* (Bäckström, 1931 and De Beer, 1937) and *Lamprophis* (Pringle, 1954). The zona annularis is a common feature of most lizards.

Anteriorly the tectum nasi is complete but posteriorly a large fenestra olfactoria advehens extends forward over almost half the length of the capsule (Fig. 3). Brock (1929) maintains that owing to the absence of the sphenethmoidal cartilage, the dorsal fenestra corresponds to the coalesced fenestra olfactoria and fissura orbito nasalis, described for *Lacerta*. For this reason she adopts Shiino's (*Crocodylus*, 1914) term: fenestra cribrosa. De Beer (1937), on the other hand, sees it exclusively as the fenestra olfactoria advehens.

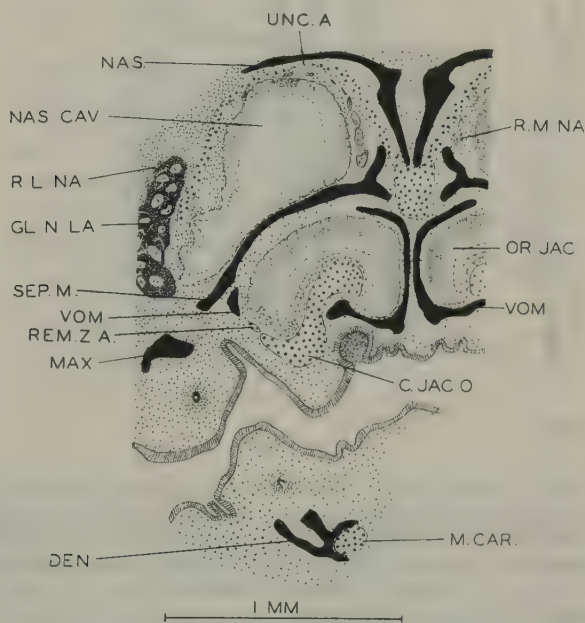


Figure 4.

Transverse section through the nasal capsule in the region of the organ of Jacobson (131 day stage)

C.JAC.O., cartilage of Jacobson's organ; DEN., dentary; GL.N.LA., glandula nasalis lateralis; MAX., maxillary; M.CAR., Meckel's cartilage; NAS., nasal; NAS.CAV., nasal cavity; OR.JAC., organ of Jacobson; REM.Z.A., remnant of the zona annularis; R.L.NA., ramus lateralis nasi V; R.M.NA., ramus medialis nasi V; SEP.M., septomaxillary; UNC.A., an unchondrified area; VOM., vomer.

Before entering the fenestra olfactoria advehens the ramus ethmoidalis V divides into two. A ramus medialis nasi passes into the capsule and then runs forward over the dorsal surface of the septomaxillary. It supplies the nasal epithelium and emerges ventrally

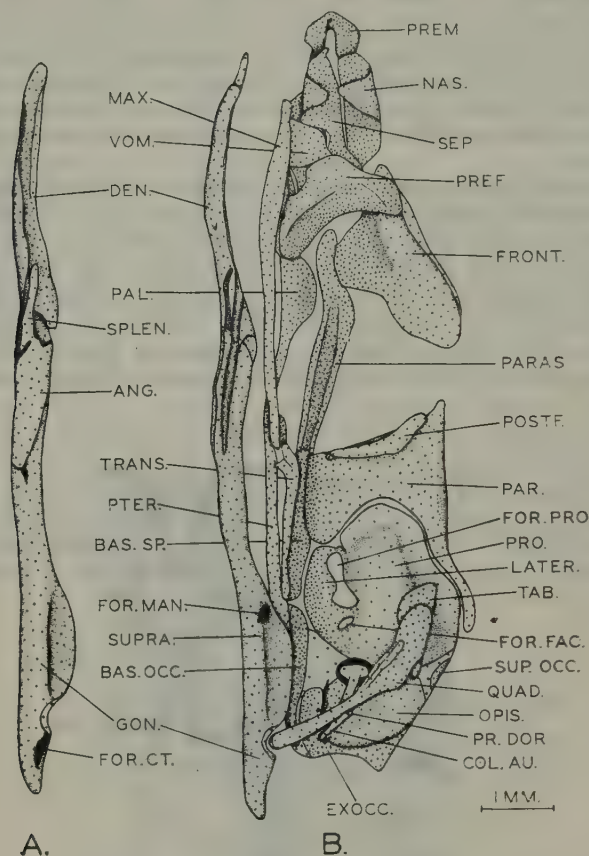


Figure 5.

A. Graphical reconstruction of the medial aspect of the lower jaw. — B. Graphical reconstruction of the lateral aspect of the skull of the 131 day stage. Nasal capsule and trabecula removed

ANG., angular; BAS.OCC., basioccipital; BAS.SP., basisphenoid; COL.AU., columella auris; DEN., dentary; EXOCC., exoccipital; FOR.CT., foramen for chorda tympani; FOR.FAC., foramen faciale; FOR. MAN., foramen for r. mandibularis V; FOR.PRO., foramen prooticum; FRONT., frontal; GON., gonial; LATER., laterosphenoid; MAX., maxillary; NAS., nasal; OPIS., opisthoticum; PAL., palatine; PAR., parietal; PARAS., parasphenoid; PRO., prooticum; POSTF., postfrontal; PR.DOR., processus dorsalis; PREF., prefrontal; PREM., premaxillary; PTER., pterygoid; QUAD., quadrate; SEP., septomaxillary; SUPRA., supra-angular; SUP.OCC., supraoccipital; SPLEN., splenial; TAB., tabular; TRANS., transversum; VOM., vomer.

to the anterior cupola and laterally to the lamina transversalis anterior, where it passes to the skin. There is therefore no foramen apicale. This is usual in snakes. The other branch of the ethmoidal nerve is the ramus lateralis nasi, and it does not enter the capsule but passes over a lateral incisura (Fig. 3) in the roof of the capsule to supply the glandula

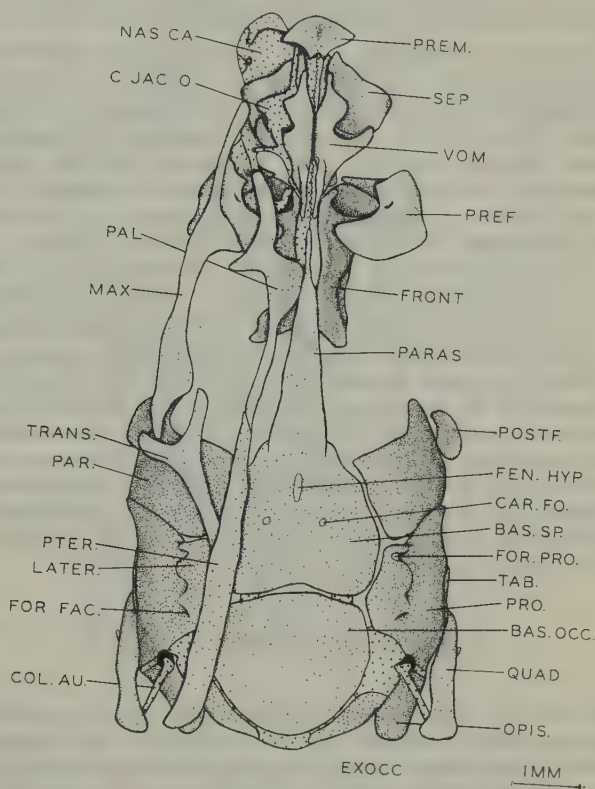


Figure 6.

Graphical reconstruction of the ventral aspect of the skull of the 131 day stage. The Maxillary, Palatine, transversum pterygoid and nasal capsule are removed from the left side

BAS.OCC., basioccipital; BAS.SP., basisphenoid; CAR.FO., carotid foramen; C.JA.O., cartilage of Jacobson's organ; COL.AU., columella auris; EXOCC., exoccipital; FEN.HYP., fenestra hypophyseos; FOR.FAC., foramen faciale; FOR.PRO., foramen prooticum; MAX., maxillary; NAS.CA., nasal capsule; OPIS., opisthoticum; PAL., palatine; PAR., parietal; PARAS., parasphenoid; PREF., prefrontal; PTER., pterygoid; PREM., premaxillary; PRO., prooticum; POSTF., postfrontal; QUAD., quadrate; SEP., septomaxillary; TAB., tabular; TRANS., transversum; VOM., vomer.

nasalis lateralis and adjacent skin. There is thus no foramen epiphaniale as in *Leptodeira* (Brock, 1929), *Vipera* (Peyer, 1912), *Dasypeltis*, *Lamprophis*, *Causus* and *Hemachatus* (Pringle, 1954). Bäckström (1931) finds in *Tropidonotus* that the tectum nasi becomes reduced in the 13 cm.

stage and the foramen epiphaniale becomes confluent with the fenestra olfactoria advehens.

Three small foramina, two on the left and one on the right side, occur in the roof of the capsule immediately in front of the fenestra olfactoria advehens (Fig. 3). Somewhat similar foramina are described for *Hemachatus* (Pringle, 1954) and *Tropidonotus* (Bäckström, 1931). The foramina are probably caused by a reduction of the tectum nasi.

The lamina orbitonasalis (also called planum antorbitale) fails to reach the nasal septum posteriorly (Fig. 3). This is a common feature of many reptiles. In *Lamprophis*, *Hemachatus*, *Dasypeltis* (Pringle, 1954) and *Leptodeira* (Brock, 1929), however, the lamina orbitonasalis is fused to the septum. Brock considers the possibility of the fusion being primary because of its persistence throughout all stages of *Leptodeira*. In *Vipera*, for instance, (Peyer, 1912) it is fused in the embryo and subsequently undergoes reduction. Brock, however, comes to the conclusion that the attachment is secondary, called forth by the delicate frame-work of the nasal region. Gaupp (1900) also regards the attachment as secondary, occurring in modified animals like mammals. Smit (1948) draws attention to the fact that the nasal capsule originates separately from the nasal septum and therefore the later attachment should be regarded as secondary. Medially, the lamina orbitonasalis curves round and forms a process which projects forward along the side of the septum nasi (Fig. 3) and is to be regarded as a remnant of a free postero-medial wall. This seems to confirm the views of Brock, Gaupp and Smit that the attachment of the lamina orbitonasalis to the septum is secondary. The lamina orbitonasalis has no maxillary process as described by Smit (1948) for *Typhlops*.

BASAL PLATE

In the 86 day old embryo a more or less rectangular plate of cartilage is suspended between the otic capsules and forms a broad platform on which the brain rests. It extends from the foramen magnum to the fenestra hypophyseos and the portion immediately behind the fenestra hypophyseos is thickened to form a crista sellaris. The oval fenestra basicranialis posterior is situated in that portion of the basal plate stretching between the facial foramen and the crista sellaris. According to Brock (1929) this portion of the plate is exceptionally long when compared with that of *Lacerta*. On each side of the fenestra basicranialis is a vacuity which Bäckström (1931) has named foramen "X". No structures pass through it. Brock (1929) regards it as an indication of reduction of the cartilaginous wall. This foramen occurs in most snakes although Pringle (1954) did not figure it for *Dasypeltis* (p. 825).

In the 131 day stage the anterior region of the basal plate (including the crista sellaris) and the hind part of the trabeculae, have ossified perichondrally as the *basisphenoid*, leaving a small oval fenestra hypophyseos in the midline immediately in front of the carotid foramina (Fig. 6). Anteriorly the basisphenoid fuses indistinguishably with a membrane bone, the parasphenoid (described under membrane bones). Backward growth of the parasphenoid-basisphenoid closes the anterior half of the fenestra basicranialis posterior.

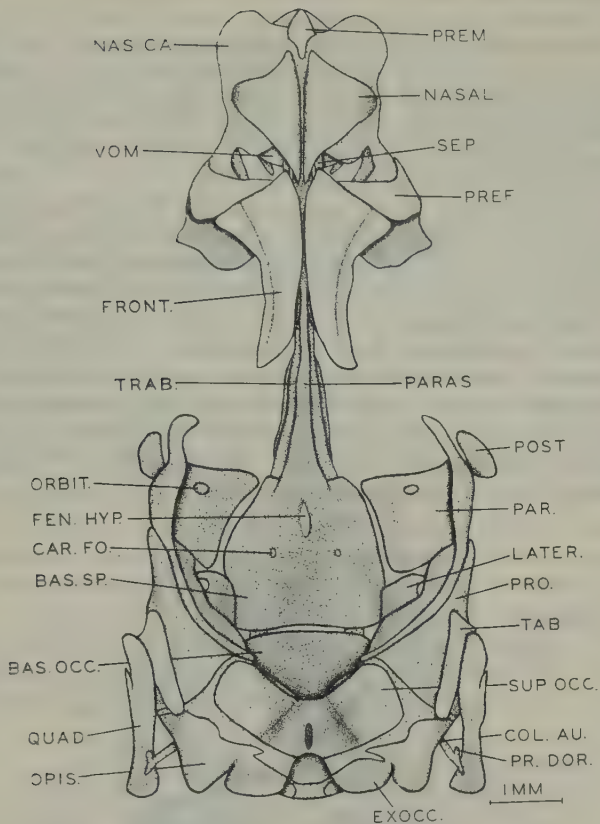


Figure 7.

Graphical reconstruction of the dorsal aspect of the 131 day stage. The maxillary, palatine and transversum are removed

BAS.OCC., basioccipital; BAS.SP., basisphenoid; CAR.FO., carotid foramen; COL.AU., columella auris; EXOCC., exoccipital; FEN.HYP., fenestra hypophyseos; FRONT., frontal; LATER., laterosphenoid; NAS.CA., nasal capsule; NASAL., nasal; OPIS., opisthoticum; ORBIT., orbitosphenoid; PAR., parietal; PARAS., parasphenoid; POST., postfrontal; PR.DOR., processus dorsalis; PREF., prefrontal; PREM., premaxillary; PRO., prooticum; QUAD., quadrate; SEP., septomaxillary; SUP.OCC., supraoccipital; TAB., tabular; TRAB., trabecula; VOM., vomer.

Posteriorly the basal plate ossifies perichondrally as the basioccipital, which in turn closes the posterior half of the fenestra basicranialis posterior. Its hind margin, which is still cartilaginous, is thickened to form the condyle. Two cartilaginous tracks, on either side of the former fenestra basicranialis posterior, are still distinguishable between the basioccipital and basisphenoid (Fig. 6 and 7); otherwise these bones are cemented together with dense connective tissue.

THE ORBITO-TEMPORAL REGION

The simplicity of this region is characteristic of all snakes. The rod-shaped paired trabeculae remain cartilaginous in the adult. They extend from the nasal septum to the antero-lateral corners of the crista sellaris. Posteriorly they gradually diverge thus leaving a triangular fenestra hypophyseos between them. The interorbital septum is absent, the skull being platyttrabic as in all snakes.

In the 86 day stage the internal carotid artery enters the skull ventrally through a foramen in what appears to be the posterior end of the trabeculae, the fenestra hypophyseos reaching very far back. In the older stage, however, the artery passes directly through a carotid foramen in the basisphenoid. De Beer (1937) and Pringle (1954) describe similar conditions for *Tropidonotus* and *Lamprophis*. In *Leptodeira* (Brock, 1929), *Dasypeltis*, *Causus* and *Hemachatus* (Pringle, 1954), however, the internal carotid enters the skull through the postero-lateral corners of the fenestra hypophyseos as in *Lacerta*. In the latter group of genera the parasphenoid thus encloses the a. carotis interna in a parabasal canal.

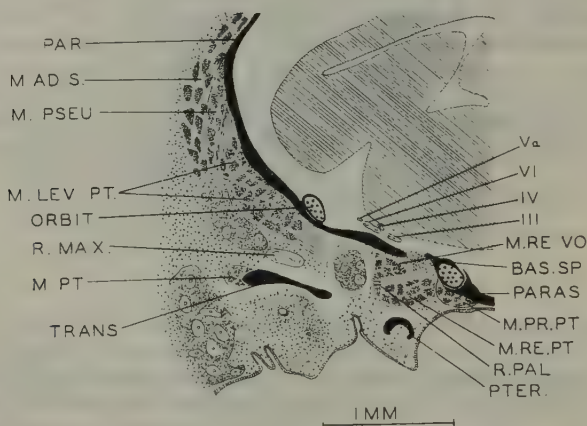


Figure 8.

Transverse section through the orbitosphenoid in the orbito-temporal region (131 day stage)

BAS.SP., basisphenoid; M.AD.S., m. adductor mandibulae externus pars superficialis; M.LEV.PT., m. levator pterygoidei; M.PR.PT., m. protractor pterygoidei; M.PSEU., m. pseudotemporalis; M.PT., m. pterygoidei; M.RE.VO., m. retractor vomeris; ORBIT., orbitosphenoid; PAR., parietal; PARAS., parasphenoid; PTER., pterygoid; R. MAX., r. maxillaris V; R.PAL., r. palatinus VII; TRANS., transversum; III., nervus oculomotorius; IV., nervus trochlearis; V a., nervus profundus; VI., nervus abducens.

An interesting feature of the orbital region of the younger stage is a pair of cartilaginous nodules situated underneath the left and right descending processes of the parietals. In the older stage they are about 170μ in length, slightly ossified perichondrally and partly

fused with the parietals (Fig. 7 and 8). As they are situated behind the nervus opticus, and anterior to the origin of the nervus oculomotorius, they must be considered as a vestige of the pila metoptica or some other part of the orbital cartilage in that region. The terminology for ossifications of the orbital region has been an object of much speculation. In his "*Studies of the Vertebrate Head*" De Beer (1926) says that the orbito-sphenoid "... is an ossification of the cranial wall, typically in front of the optic foramen ..." (p. 362). He further states: "The pila prootica and pila metoptica of *Sphenodon* and *Lacerta* remain cartilaginous, but the latter may ossify in some forms in which case the bone, being a post-optic part of the original skull wall, may be a laterosphenoid. It may, on the other hand, be a modified orbitosphenoid" (p. 363). According to Bellairs (1949 b): "Paired ossifications above and immediately behind the optic nerves (i.e. of the pila metoptica, taeniae mediales, planum supraseptale, etc.) are termed orbitosphenoids; those situated more posteriorly (i.e. ossifications of the pile antotica) have been termed laterosphenoids or pleurosphenoids" (p. 491). Parker (1879) described paired orbitosphenoids above the trabeculae in the mid-orbital region of an adult *Tropidonotus*. In 1949, Parker's findings were confirmed when Bellairs (1949 a) described a pair of cartilaginous nodules above the trabeculae, in the mid-orbital region of a 7.2 mm. embryo of *Vipera berus*. After tracing similar cartilaginous nodules in some embryos of *Causus*, Pringle (1954) writes: "These orbital cartilages are apparently spasmodic in occurrence and usually unequal (sic) in size, but once present are persistent" (p. 840).

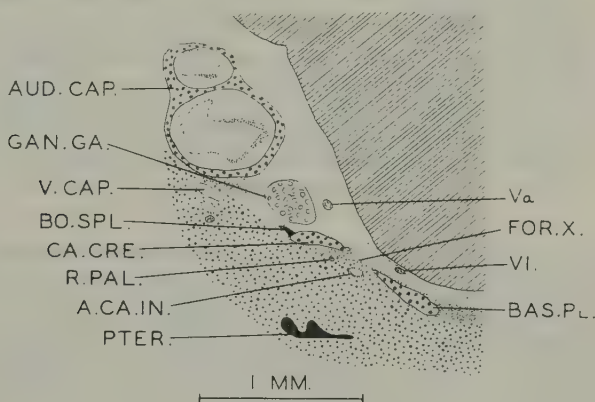


Figure 9.

Transverse section through the orbito-temporal region of the 86 day stage (same region as in Fig. 10)

A.CA.IN., a. carotis interna; AUD.CAP., auditory capsule; BAS.PL., basal plate; BO.SPL., bony splinter on cartilaginous crest; CA.CRE., cartilaginous crest on basal plate; FOR.X., foramen x; GAN.GA., ganglion Gasser; PTER., pterygoid; R.PAL., ramus palatinus; VII; V.CAP., v. capitis lateralis; Va., n. profundus; VI., n. abducens.

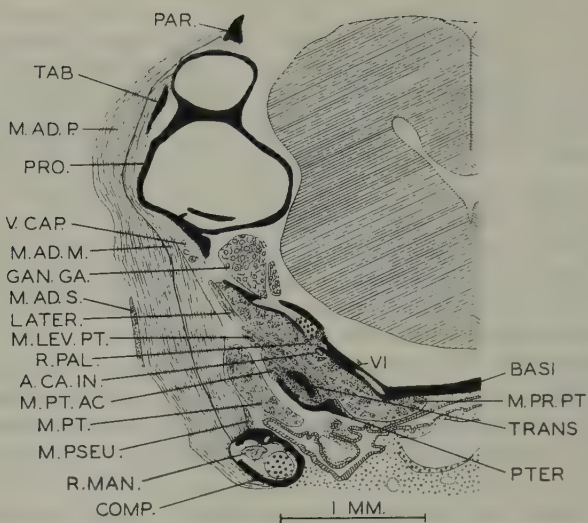


Figure 10.

Transverse section through the laterosphenoid in the orbito-temporal region (131 day stage)

A.CA.IN., a. carotis interna; BASI., basisphenoid; COMP., composite bone (gonial + supra-angular); GAN.GA., ganglion Gasseri; LATER., laterosphenoid; M.AD.M., m. adductor mandibulae externus pars medialis; M.AD.P., m. adductor mandibulae externus pars superficialis; M.LEV.PT., m. levator pterygoidei; M.PSEU., m. pseudotemporalis; M.PT., m. pterygoideus; M.PT.AC., m. pterygoideus accessorius; M.PR.PT., m. protractor pterygoidei; PAR., parietal; PRO., prooticum; PTER., pterygoid; R.MAN., ramus mandibularis V; R.PAL., ramus palatinus VII; TAB., tabular; TRANS., transversum; V.CAP., v. capitis lateralis; VI., nervus abducens.

In the region of the incisura prootica of the 86 day stage of *Thelotornis* a distinct crest of cartilage projects dorsolaterally from the basal plate. A splinter of bone extends dorsally from this cartilaginous crest (Fig. 9), but it is difficult to say whether this bone is of cartilaginous origin or not. "It is . . . conceivable that the cartilaginous stage has been suppressed and that the bone is laid down in dense mesenchyme which represents the cartilaginous stage." (Brock, 1929. p. 316.) In the older stage of *Thelotornis*, the cartilaginous crest has ossified separately from the basal plate and has merged with the bone on its dorsal edge (Fig. 10). This bone forms a distinct line of suture with the parasphenoid-basisphenoid ventrally and extends dorsally and diagonally across the prootic incisure. Its anterior edge fuses with the prootic, (probably with a projection from the prootic), separating the nervus profundus on its medial side from the ramus maxillaris V and ramus mandibularis V on its lateral side. Posteriorly it is in synostosis with the cochlear part of the otic capsule. The latter two nerves pierce a membrane which extends from the parietal to the basal plate, lateral to the bone.

There has been much discussion regarding the homology of this bone. Parker (1879) called it the alisphenoid while Peyer (1912) described it as a prootic extension. Gaupp (1902) considers the dura mater as representing the original cranial wall. The bone in question is somewhat removed from the dura mater and therefore Gaupp considers it as being extracranial. De Beer (1926) points out that the dura mater and perichondrium have become separated. The former is internal to the trabeculae, basal plate and otic capsule and therefore cannot represent the primitive skull wall. The space between them is epidural, "it may be considered as intramural but not extracranial" (p. 316). De Beer's conclusion is thus more acceptable: "It is not a processus ascendens, for it does not arise from and has no relation with the pterygoquadrate. It is not a pila prootica, because it lies behind the profundus; it is not a pila lateralis as in *Amia*, for it is situated median to the vena capitis lateralis . . . The only other element with which it might be compared is the post profundus portion of the laterosphenoid of the bird" (p. 315). In 1929 Brock (*Leptodeira*) regarded the bony structure ("Gaupp's bone") on the cartilaginous crest ("basitrabecular process") as an epipterygoid which is incorporated in the cranial side wall. After studying the skull of *Acontias* (1941) she modified her opinion: *Acontias* has a similar process but is has a typical Lacertilian epipterygoid and basitrabecular process. She then re-examined a late stage of an embryo of *Leptodeira* and found that this was a discrete bone, wedged in between the otic capsule and basal plate and forming a suture with the parasphenoid-basisphenoid. She then agreed that the name laterosphenoid was the best one to use, "signifying that this is an ossification in the membrane of the true cranial side wall, and not a splanchnocranial element" (p. 86).

The foramen faciale for the exit of the nervus facialis, is separated anteriorly from the foramen prooticum by a prefacial commissure. The ramus palatinus VII runs forward and ventrally outside the skull wall. A small branch of the nervus trigeminus continues in a ventral direction, buried in thickened tissue outside the laterosphenoid, and joins the ramus palatinus. It is therefore a commissure between the anterior portion of the ganglion Gasserii (probably ramus maxillaris V) and the ramus palatinus VII. The ramus hyomandibularis VII will be described in connection with the columella auris (see p. 165).

The nervus abducens originates below the ganglion acousticum and in the region of the crista sellaris it passes anteriorly in a canal excavated in the lateral edge of the basisphenoid. Anteriorly the canal opens into the space between the dura mater and the descending process of the parietal. From here it continues anteriorly in company with the n. profundus, n. oculomotorius and n. trochlearis. Gaupp (1902) explains that in lizards these nerves pass through various foramina, while in snakes the descending process of the parietal forms an additional wall outside the original primitive skull wall, causing the nerves to pass in a common passage. These nerves leave the skull through a common foramen orbitale magnum.

The a. carotis interna runs anteriorly lateral to the skull wall. It passes underneath the columella auris, and the a. orbitalis branches off immediately behind the foramen faciale. The main branch enters the cranial cavity from a ventral direction as already described.

The v. capitis lateralis passes backwards lateral to the laterosphenoid receiving a medial branch, lying between the dura mater and the side wall, in the hind corner of the foramen prooticum. It continues posteriorly, dorsal to the shaft of the columella auris.

OTIC REGION

86 day stage (*Chondrocranium*)

Ventrally the auditory capsule is attached to the lateral edge of the basal plate by means of an extensive basivestibular commissure. The cochlear part of the auditory capsule compresses the side of the basal plate, so that the basivestibular commissure rests partly on the basal plate and partly on the otic capsule. Immediately in front of the commissure there is the facial foramen, separated from the incisura prootica by a slender prefacial commissure. Posteriorly the basivestibular commissure extends to the anterior end of the fissura metotica. Dorsally the capsules are interconnected by a tectum synoticum. An unchondrified area (Cp. *Causus*, *Haemachatus* (Pringle, 1954), *Leptodeira* (Brock, 1929), *Vipera* (Peyer, 1912), *Eumeces* (Rice, 1920)), is observable in the dorsal surface of the capsule, immediately in front of the tectum synoticum.

131 day stage

Pringle, Peyer, Bäckström and De Beer (op. cit.) describe two bony components in the otic capsule of the snakes examined by them: the opisthoticum and prooticum. The prooticum lies anterior to the fenestra ovalis (vestibuli) and the opisthoticum behind it; together they form a rim which encircles the fenestra. The process of ossification has not been completed in the capsule of this stage, but an unossified strip of cartilage in the region of the fenestra ovalis (Fig. 6 and 7) may be considered as the boundary between the prooticum and the opisthoticum. Haas (1930) and Smit (1948) could trace only one element, the prooticum in the otic capsule of *Typhlops*.

The three semicircular canals are clearly demarcated as prominences on the external surface of the capsule. The anterior semicircular canal forms a very prominent ridge along the dorsal margin, while parallel grooves on the lateral and medial surfaces indicate the course of the anterior septum. The lateral semicircular canal is also clearly recognizable on the lateral surface. The unchondrified area present in the dorsal surface of the capsule of the younger embryo is now closed with dense connective tissue.

The interior of the otic capsule of *Thelotornis* is very similar to that of *Causus* (Pringle, 1954), but also agrees closely with the description of *Vipera* (Peyer, 1912) and *Leptodeira* (Brock, 1929). There is a large vestibular cavity, completely separated from the anterior semicircular canal by a strong septum vestibulare anterius. The cavum cochleare joins the ventral portion of the vestibular cavity. The septum between the anterior and posterior portions of the vestibular chamber is absent. The septum posterius and laterale are weakly developed.

A large foramen acusticum is situated in the median wall of the capsule, immediately behind and above the foramen faciale. The

foramen is incompletely separated into an anterior and posterior portion by a splinter of bone, projecting dorsally from the medio-anterior wall of the cochlear capsule. The anterior and posterior branches of the acoustic nerve enter the capsule separately through the foramen. This incompletely divided foramen acusticum is probably an exceptional feature in snakes, because Peyer (1912) is the only author who describes "ein grosses, noch einheitliches Foramen acusticum" (p. 571) in a 70 mm. stage of *Vipera*. In the 125 mm. stage of *Vipera*, however, the acoustic foramen is completely subdivided into anterior and posterior foramina.

The foramen for the ductus endolymphaticus is situated immediately dorsal and posterior to the acoustic foramen.

The boundary between the otic and occipital region is indicated by the fissura metotica. The anterior end of the fissura widens out to form the recessus scalae tympani. This anterior division is separated from the rest of the fissura by a bony projection from the capsule. The projection comes into close contact with the basioccipital without fusion. The posterior division of the fissura is known as the foramen jugulare (Gaupp, 1900).

The recessus scalae tympani leads into the cochlear cavity by the fenestra cochleae, in the posterior floor of the cochlear capsule; into the cranial cavity by a medial opening; and to the exterior by its lateral opening. The ductus perilymphaticus leads out through the fenestra cochleae into the recessus scalae tympani.

According to Gaupp (1900) the usual course of the n. glossopharyngeus of reptiles is through the recessus scalae tympani division of the fissura metotica, i.e. extracapsular. In snakes, however, authors record a curious variation. In *Thelotornis* the nerve passes into the otic capsule through a fenestra glossopharyngeus interna, situated in its medial wall immediately above the median aperture of the recessus scalae tympani. Its exit is through the fenestra cochleae and the lateral aperture of the recessus scalae tympani. A similar intracapsular course was described for *Tropidonotus* (Bäckström, 1931), *Dasypeltis* and *Causus* (Pringle, 1954). According to Rice (1920) the "undetermined" nerve, which Peyer (1912) described for *Vipera*, is actually the nervus glossopharyngeus, which also penetrated the medial wall of the otic capsule. The n. glossopharyngeus of *Leptodeira* (Brock, 1929) penetrates the basal plate immediately below the medial aperture of the recessus scalae tympani. Its exit is in close proximity to the jugular foramen. Brock states: "The course is the normal reptilian one, through the recessus scalae tympani, the only variation being that the margin of the basal plate has surrounded it." (p. 195). Rice (1920) gives a similar explanation for the intracapsular course of this nerve in some lizards. He maintains that it is due to a gradual extension of the otic cartilage, resulting in a narrowing of the fenestra cochleae. According to Pringle (1954) the usual course for the nervus glossopharyngeus is through the jugular foramen such as he described for *Lamprophis* and *Hemachatus*.

The vagus nerve passes through the jugular foramen, but as in *Leptodeira* (Brock, 1929) no jugular vein accompanies it. Gaupp (1900) homologized a vein, which passes through this foramen in the embryo *Lacerta*, with the mammalian internal jugular. Rice (1920) confirm Gaupp's observations after examining *Eumeces*.

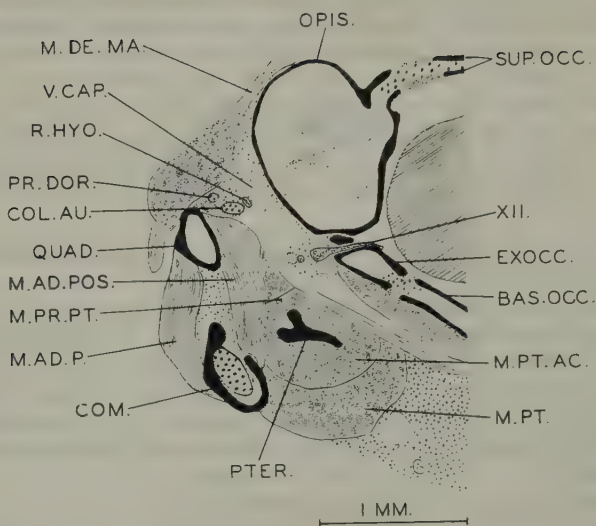


Figure 11.

Transverse section through the otic region immediately in front of the suspensorium

BAS.OCC., basioccipital; COL.AU., columella auris; COM., composite bone (gonial and still cartilaginous articular); EXOCC., exoccipital; M.AD.P., m. adductor mandibulae externus pars profundus; M.AD.POS., m. adductor mandibulae posterior; M.DE.MA., m. depressor mandibulae externus; M.PR.PT., m. protractor pterygoidei; M.P.T., m. pterygoideus; M.PT.AC., m. pterygoideus accessorius; OPIS., opisthoticum; PR.DOR., processus dorsalis; PTER., pterygoid; QUAD., quadrate; R.HYO., r. hyomandibularis VII; SUP.OCC., supraoccipital; V.CAP., v. capitis lateralis; XII., n. hypoglossus.

COLUMELLA AURIS

The columella auris consists of a slender, still cartilaginous (131 day stage) rod with its footplate inserted in the fenestra ovalis of the cochlear capsule. The columella projects backwards in a ventro-lateral direction and comes into close contact with the postero-median surface of the quadrate. A small process projects dorsally from the distal end of the columella and is syndesmotically attached to the hind surface of the quadrate (Fig. 5 and 11). This structure has been regarded as a "stylohyale" by Parker (1879) and as a processus internus by Bäckström (1931). According to Brock (1929) the distal end of the columella of *Leptodeira* "bends sharply from the axis of the proximal end, and continues in a posterior and ventral direction" (p. 305). This portion of the columella she homologized with the processus dorsalis of other reptiles and a process on its distal end, which fuses with a projection from the quadrate, with the intercalare. She also regarded the connexion with the quadrate as secondary and therefore recalling the condition

of crocodiles. As there is no backwardly bent distal end in the columella of *Thelotornis*, and as the processus internus is of less general occurrence in reptiles such as *Gekkonidae*, *Scincidae*, *Uroplatidae*, *Anguidae*, *Sphenodon* (Versluijs, 1898 and 1903), I would rather homologize the process on the distal end of the columella with the processus dorsalis. This was also the view of De Beer (1937) and Goodrich (1930).

The r. hyomandibularis VII passes back dorsally to the columella and medial to the dorsal process. Posteriorly and ventrally to the columella the chorda tympani branches off from the r. hyomandibularis and continues ventrally to enter the primordial canal of the lower jaw medially (Fig. 5). This is the usual course for the r. hyomandibularis and chorda tympani in snakes. According to De Beer (1937) the absence of an extracolumella in snakes allows the chorda tympani to take this direct course.

OCCIPITAL REGION

In the 86 day stage the pilae occipitales arise from the postero-lateral corners of the basal plate and extend upwards and outwards into the tectum synoticum. Even in the 131 day stage the exoccipitals lie far apart dorsally, the supraoccipital forming the dorsal border of the foramen magnum (Fig. 7). In adult snakes generally, the exoccipitals meet dorsally and exclude the supraoccipital from the foramen magnum. It is, thus, difficult to say whether the occipital region participates in the formation of the tectum synoticum to form a tectum posterius. Gaupp (1906, *Tropidonotus*) writes as follows: "Durch Verknorpelung des Deckengewebes zwischen beiden Ohrkapseln entsteht das Tectum synoticum, in das die oberen Enden beider Occipitalpfeiler übergehen. Das Tectum scheint hier zum Teil der Occipitalregion zugerechnet werden zu müssen" (p. 793). This view was confirmed by Peyer (1912) for *Vipera*. Bäckström (1931, *Tropidonotus*) could not confirm this view because according to him a definitive tectum posterior is formed quite late in the ontogeny. "Bei der Verknöcherung der pila occipitalia wird kaudalwärts von dem 'Tectum synoticum' durch Vereinigung der beiden Pleurooccipitalia auch ein 'Tectum posterior' gebildet" (p. 125). In the 86 day stage of *Thelotornis* the cartilage connecting the otic capsules shows no sign of ossification, while the pilae occipitales (future exoccipitals) are well ossified perichondrally. The occipital region therefore does not participate in the formation of the cartilaginous tectum. If snakes possess a tectum posterius at all, they acquire it only as extensions of the ossified exoccipitals, in which case the term tectum posterius is probably inadmissible.

Ventrally and posteriorly the *exoccipitals* are separated from the opisthoticum, but dorsally they are in synchondrosis with it. Ventrally the anterior portion of the exoccipital is slightly ossified perichondrally, and the remaining cartilage is continuous with the still unossified area in the region of the basivestibular commissure (Fig. 6). The hypoglossal nerves pass through 2 pairs of foramina in the postero-lateral corners of the exoccipitals.

The *supraoccipital* ossifies medially in the tectum synoticum and extends laterally into the roof of the otic capsule on each side (Fig. 7). Parker (1879, *Tropidonotus*) calls these lateral wings epiotica. After studying the development of *Tropidonotus*, Bäckström (1931) finds that

this "Deckknochen (supraoccipitale) ist in seiner Anlage vollständig einheitlich". A tract of sutural cartilage separates the supraoccipital from the prootics, opisthotics and exoccipitals. An unossified spot, filled with dense connective tissue, occurs in the midline of the supraoccipital.

The *basioccipitals* have already been described in connexion with the basal plate.

QUADRATE AND LOWER JAW

The dorsal component of the mandibular arch is represented by a long slender bar, the quadrate. It is vertical in position and projects slightly backwards and outwards to the lower jaw. The broad dorsal portion of the quadrate is syndesmotically attached to the tabular. It also possesses a lateral ridge (Fig. 5) to which the m. adductor mandibulae externus is partially attached. The ventral portion of the quadrate is more slender and articulates with a concave facet on the lower jaw.

The ventral component of the mandibular arch is represented by a long slender, slightly curved cylindrical rod, the cartilage of Meckel. The posterior portion of Meckel's cartilage ossifies perichondrally as the *articular*. The following membrane bones occur: dentary, splenial (opercular), angular and a large composite bone [fused gonial (dermarticular), supra-angular and a cartilage bone, the articular].

The teeth-bearing *dentary* is situated ventro-lateral to Meckel's cartilage and occupies the anterior third of the jaw. Posteriorly the lateral edge of the dentary curves outwards and forms a posterior tapering elongation, which reaches far backwards and lies lateral to the composite bone (supra-angular) (Fig. 5 B).

The *splenial* lies on the inner surface of Meckel's cartilage and its dorso-posterior edge is in synostosis with the angular (Fig. 5A). The younger stage of *Thelotornis* shows separate anlagen of these bones.

The *angular* lies on the medial surface, anterior to the gonial, and slightly overlaps the anterior edge of the composite bone.

In the younger stage the *gonial* extends backwards along the medial surface almost to the posterior end of Meckel's cartilage. In the region of the articulation it also appears on the outer surface.

The *supra-angular* covers Meckel's cartilage laterally. It extends anteriorly from the dentary to the region immediately in front of the articulation. Posteriorly it forms a prominent dorsal process, a functional processus coronoideus, for attachment of the m. adductor externus. A foramen in the supra-angular allows for the passage of the r. mandibularis V into the primordial canal, which also houses Meckel's cartilage and the chorda tympani VII. The chorda tympani enters the canal through a foramen on the medial surface of the processus retro-articularis.

The anterior portions of the left and right cartilages of Meckel project in front of the dentary and are connected with a ligament which allows free movement between the two halves of the lower jaw. The absence of a lower jaw symphysis is general for snakes, although in the fossorial *Typhlops* the antero-medial portions of Meckel's cartilage are fused (Smit, 1949).

Similar bony components in the lower jaw were described for *Tropidonotus* (Gaupp, 1911 and Bächström, 1931). After examining the

lower jaw of *Vipera*, Bäckström (1931) came to the conclusion that it agrees with that of *Tropidonotus*. According to Bäckström, Peyer (1912) described the angular of *Vipera* erroneously as the complementary and a portion of the gonial as the angular. Brock (1929) could not find a separate angular in *Leptodeira*. In addition to these components Smit (1948) and De Beer (1937) identified a separate coronoid for *Typhlops*, and *Tropidonotus* respectively.

MEMBRANE BONES

The Palate and Skull Base

According to Fuchs (1908) the "primäre Munddach" is formed by the "primitiven Gaumen, den Oberkiefermassen, dem Nasenseptum und der primären Rachendecke" (p. 166). A mammalian or crocodilian secondary palate is absent in snakes, but a "sekundärer Gaumen" is formed behind the orifice of Jacobson's organ (posterior boundary of the "primitiven Gaumen") as "... einer bedeutenden Aufwärtswanderung des Vomerpolsters und einer ausgedehnten Verwachsung desselben mit den Oberkiefermassen auf Kosten der vorderen und mittleren Teile der absteigenden Choanengangschenkel und der Choanenspalten" (Fuchs, 1908, p. 212).

The fused *premaxillaries* form the anterior border of the skull and palate. A deep groove occurs between the alveolar portion and the ascending process (Fig. 5). The anterior horizontally flattened nasal septum fits into this groove. Anteriorly the nasal capsule is thus well supported by the premaxillary. The ascending process of the premaxillary bends over caudally to become wedged in between the diverging anterior tips of the nasals (Fig. 7). Ventrally the palatine process is syndesmotically attached to the septomaxillary. The premaxillary bears the egg tooth.

The *septomaxillary* is well developed as in all snakes. Anteriorly it borders on the premaxillary, while its posterior limits adjoins the antero-medial edge of the frontal. The latter suture acts as a hinge in which the nasal region articulates with the orbital region (see under Kinesis). The septomaxillary forms the anterior and dorsal walls of the capsule containing Jacobson's organ. Because it reaches from the nasal septum to the side wall of the nasal capsule it also forms a bony floor for the nasal sac in this area (Fig. 4). Its lateral edge curves dorsally, thus contributing to the lateral wall (Fig. 5).

The elongated *maxillary* represents the secondary upper jaw. Posteriorly it forms a hinge-joint with the bifurcated transversum (ectopterygoid). Anteriorly it forms a medial projection which is ligamentally attached to the ventral surface of the prefrontal (Fig. 6). The maxillary is not in contact with the premaxillary as in primitive snakes.

The paired *vomers* are syndesmotically interconnected. The anterior portion of the vomer forms the ventral and medial walls of the capsule containing Jacobson's organ. Posteriorly the organ extends into a pocket formed by the vomer (Fig. 4 and 6). The concave plate of the cartilage of Jacobson's organ covers the incisure on the ventro-lateral surface of the vomer, leaving an opening between them through which

Jacobson's organ opens into the mouth cavity. Branches of the nervus olfactorius pass from the epithelium of Jacobson's organ through perforations in the dorsal surface of the vomer. Behind Jacobson's organ the vomer continues backwards as a vertical bar. A branch of the r. maxillaris V is in a medial position, with regards to the vomer, after passing through a foramen in the bar. This vertical bar tapers posteriorly, and terminates ventral to the nasal septum in the region of the lamina orbitonasalis.

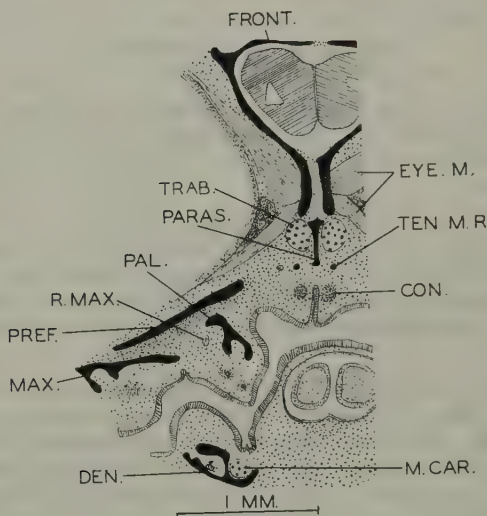


Figure 12.

Transverse section through the anterior region of the orbit

CON., dense connective tissue between vomer and the medio-dorsal projection of the palatine; DEN., dentary; EYE M., eye muscles; FRONT., frontal; M. CAR., Meckel's cartilage; MAX., maxillary; PAL., palatine; PARAS., parasphenoid; PREF., prefrontal; R. MAX., r. maxillaris V; TEN. M. R., tendon of the m. retractor vomeris; TRAB., trabecula.

The *palatine* is a dagger-shaped bone. The medio-dorsal extension curves over the nasopharyngeal passage and presses against the ventral surface of the parasphenoid. This extension of the palatine is connected to the posterior process of the vomer by a dense tract of connective tissue (Fig. 12). A lateral extension is in syndesmosis with the medial projection of the maxillary.

Anteriorly the slender *pterygoid* slightly overlaps the posterior tip of the palatine and is in firm syndesmosis with it. The pterygoid extends to the suspensorial part of the quadrate to which it is ligamentally attached.

The pterygoid and maxillary is interconnected with a flat, anteriorly bi-furcated bone, the *transversum* (ectopterygoid). Connective tissue connects the posterior tip of the maxillary to the lateral prong of the transversum, while the medial prong similarly attaches to a

medial prominence of the maxillary (Fig. 6). The transversum gradually slopes backwards and inwards to the pterygoid, its posterior end fitting into a groove on the dorsal surface of the pterygoid.

The palatine, maxillary and anterior half of the pterygoid all bear teeth, while the poison fangs are located on the posterior knob of the maxillary (teeth not yet attached to the bones in the 131 day stage).

The *parasphenoid* is the only membrane bone of the skull base and it occludes the fenestra hypophyseos. Anteriorly it commences as a vertical bar (Fig. 12), but it gradually flattens posteriorly. Its forceps-shaped lateral edges enclose the trabeculae (Fig. 8). Posteriorly the parasphenoid is indistinguishably fused with the basisphenoid.

Fuchs maintains: "Da in primitiven Gaumen, wie allgemein bekannt, von Knochen nur die Praemaxillaria entstehen . . .". In *Thelotornis*, however, the vomers also extend forward into this region of the palate. A similar condition was described for *Monopeltis* (Kritzinger, 1945) and *Acontias* (De Villiers, 1939) where the vomers as well as the maxillary extend into this region.

Circumorbital Bones

The anterior portion of the *prefrontal* forms a vertical arch over the postero-lateral wall of the cartilaginous nasal capsule. Posteriorly it becomes laterally concave, thus separating the orbit from the nasal region. A foramen for the nasolacrimal duct perforates the prefrontal ventro-laterally. The dorsal edge of the prefrontal overlies the frontal and is syndesmotically attached to it.

The orbit is bordered posteriorly by a sickle-shaped bone, the *postfrontal* (Fig. 5). Its ventral tip is connected to a lateral process on the parietal by means of an extensive ligament.

The above-mentioned circumorbital bones are also present in *Tropidonotus* (Bäckström, 1931) and *Vipera* (Peyer, 1912). A third component of this series, the supra-orbital, occurs in *Typhlops* (Smit, 1948) and *Python* (Hoffman, 1890).

Temporal Bones

A small splint-like bone, the *tabular*, occurs on the lateral surface of the prooticum, medial to the dorsal surface of the quadrate. Mutual movement is possible between these bones. The homology of the single temporal bone in snakes has been the object of frequent discussion. Peyer (1912) and Bäckström call it a squamosal, Pringle (1954) calls it a supratemporal, while Brock (1935) concludes that it is a tabular. Brock states: "In those lizards in which two temporal elements are present, the outer squamosal has its position on the lateral aspect of the quadrate head, while the tabular (supratemporal) is wedged between the quadrate and the otic capsule . . . The large temporal muscle is always attached to the squamosal and not to the tabular, which is a bone of the occiput; in those forms where the outer bone, the squamosal, has been lost, e.g. the Gecko's, the temporal muscle passes over the tabular with no attachment of fibres and becomes attached to the parietal" (p. 202). This is also the condition in *Thelotornis*. The bone is therefore not a squamosal, Brock agrees with Williston and Broom in calling it a tabular and not a supratemporal, because ". . . the supratemporal element of

Seymouria is lost in Cotylosaurs and all higher reptiles, while the more posterior tabular, a bone of the occiput and articulating with the quadrate, is retained in Squamata, as well as Cotylosaurs and Therapsids" (p. 203).

Cranial Roof

As in all specialized snakes like the *Colubridae*, *Dasypeltidae*, *Viperidae* and *Elapidae*, the paired *nasals* cover only a small portion of the nasal capsule (Fig. 7). The anterior tips of the nasals are pushed apart by the caudal projection of the premaxillary. Posteriorly they terminate immediately ventral to the anterior edge of the frontals. Medially they dip into the trough between the nasal capsules. The nasals are interconnected by connective tissue.

The *frontals* are large bones in the orbital region (Fig. 5, 6 and 7). Their lateral descending processes approach each other above the trabeculae and parasphenoid, thus enclosing the olfactory lobes in a bony capsule (Fig. 12).

Between the frontals and the supraoccipitals the brain is roofed over by the *parietals*. Even in the 131 day stage of *Thelotornis* the parietals are still weakly developed. The large dorsal fontanella which only closes a long time after the embryo is hatched, is still wide open. In front of the otic capsule the parietals have downgrowths which meet the lateral edges of the parasphenoid-basisphenoid (Fig. 5 and 8).

The downgrowths of the parietals and frontals obliterate the cartilaginous interorbital septum. This condition is not only found in snakes, but also in some fossorial Lacertilia such as *Acontias* (Brock, 1941) and *Monopeltis* (Kritzing, 1945). The eye muscles attach to this secondary interorbital septum.

A wide gap still occurs between the frontals and parietals. In adult snakes, however, these bones are dorsally approximated leaving only a foramen orbitale magnum between their downgrowths (Gaupp, 1902).

KINESIS

Although the trigeminus muscles of *Thelotornis* agree with those of the other Opisthoglypha, which Haas (1930, 1931) discussed in detail, it seems advisable to describe some important muscles, before proceeding to a description of the kinesis.

Musculus Adductor Mandibulae Externis

Pars superficialis. Arises from the posterior edge of the postfrontal and parietal immediately behind the postfrontal. The fibres pass ventro-caudally to the latero-ventral surface of the composite bone of the lower jaw.

Pars medialis. Arises from the parietal above the otic capsule; some fibres arise from the otic capsule itself. The muscle passes downwards over the tabular to the dorso-lateral surface of the lower jaw (Fig. 10). The ramus mandibularis V emerges immediately behind the pars medialis and continues in a ventral direction medial to the pars profunda.

Pars profunda. Fits into the angle between the quadrate and lower jaw and is distinctly divided into three portions. They originate from the quadrate. The anterior fibres are also attached to the parietal and otic capsule, but pass freely over the tabular. The medial portion is the only one to insert on the medial surface of the lower jaw, the others insert on the lateral surface. Lakjer (1926) described the medial portion as a separate muscle, the *m. adductor mandibulae posterior*. Haas (1930), however, regards it "als ein mehr medial gelegener Anteil des Adductor externus" (p. 101).

Musculus Adductor Mandibulae Internus

The *m. pseudotemporalis* is a thin muscle, which arises from the parietal and descends to the dorso-lateral surface of the lower jaw. The ramus maxillaris V emerges immediately behind the muscle and passes forward lateral to it. According to Haas (1930) the *m. pseudotemporalis* is chiefly a "Mundwinkelspanner. Als protrahierend kommt er aber kaum in Betracht" (p. 103).

The *m. pterygoideus* arises from the lateral prong of the transversum and passes backwards ventro-lateral to the main body of the bone. A dorsal portion (*m. pterygoideus accessorius*) is attached along the length of the ventral surface of the pterygoid. Posteriorly it inserts onto the medial surface of the processus retro-articularis and the lower jaw, immediately in front of the suspensorium. It is obvious that the *m. pterygoideus* pulls the lower jaw chiefly medially and that its adduction function is much reduced.

Musculus Levator Palati Quadrati

The *m. levator pterygoidei* arises from the lateral surface of the parietal and from a strong ligament, which attaches the ventral edge of the postfrontal to the parietal. The muscle passes obliquely backwards underneath the r. maxillaris V to the dorso-medial surface of the pterygoid. Some fibres arise dorsally from the parietal and otic capsule and pass in a ventral direction. These fibres are attached to the fascia of the main portion.

Anteriorly the *m. protractor pterygoidei* is attached to the parasphenoid-basisphenoid and laterosphenoid. Posteriorly it is inserted onto the dorsal surface of the pterygoid. A separate portion also attaches to the medial surface of the quadrate and lower jaw in the region of the suspensorium. Lakjer (1926) calls it the *m. protractor quadrati*.

Posteriorly the *m. retractor pterygoidei* originates from the ventral edge of the parietal and parasphenoid-basisphenoid, lateral to the origin of the *m. protractor pterygoidei*. Anteriorly it is inserted onto the medial extension of the palatine.

The *m. retractor vomeris* seems to be a separate slip of the *m. retractor pterygoidei*. It originates from the skull base, anterior to the origin of the *m. retractor pterygoidei*. Anteriorly it is inserted by means of a long, thick tendon (Fig. 12) on the dorso-posterior edge of the vomer. The tendon is also associated with the dorso-medial extension of the palatine.

The Mechanism of Kinesis

The dorsally directed rotation of the nasal region is facilitated by a mesokinetic "Beugungslinie", situated between the nasal, septomaxillary and prefrontal on the one side and frontal on the other. No movement is possible between the frontal and parietal or the parietal and otico-occipital region.

The opening of the mouth commences with the contraction of the m. depressor mandibulae group, which depresses the lower jaw.

The process of kinesis commences with the contraction of the m. levator pterygoidei and m. protractor pterygoidei. The pterygo-palatine bar is lifted and pulled forward powerfully. The m. protractor pterygoidei contracts and pulls the quadrate and lower jaw slightly forward. The transversum transfers the movement to the maxillary. Owing to its connexion with the prefrontal, the forward movement of the maxillary is delimited; therefore its posterior portion is pushed ventrally and laterally. Anteriorly the maxillary rotates on a transverse axis on the ventral surface of the prefrontal.

The medio-dorsal process of the palatine lies rather far (624μ) away from the posterior process of the vomer (Fig. 5), but further ossification in later stages would be possible in the dense connective tissue stretching between the two bones (Fig. 12). If this ossification takes place, the condition would be similar to that of *Tropidonotus* (Bäckström, 1931). The palatine would then push against the vomer and the nasal region would be raised. According to Haas (1930) the prefrontal is rotated by the palatine and maxillary, but the other bones anterior to the prefrontal remain stationary. "Das macht es verständlich, dass im Gegensatz dazu den intrakraniellen Bewegungen eine verhältnismässig geringe Bedeutung zukommt" (p. 106). In *Thelotornis* the palatine is not ligamentally attached to the prefrontal. It is, however, obvious that the raising of the nasal region must be brought about by the palatine pushing against the vomer. The septomaxillary-frontal joint acts as a hinge. The palatine and maxillary now assume a more vertical position, and the backward curving teeth including the poison fangs are at a favourable angle to get a good grip on its prey.

The m. levator pterygoidei also pulls the pterygoid (and therefore also the transversum and maxillary) in a lateral direction. This causes a widening of the orifice of the mouth.

The closing of the mouth is the result of the contraction of the m. adductor mandibulae externus group and of the m. pseudotemporalis. When the m. retractor pterygoidei, m. retractor vomeris and m. pterygoideus contract, the palatine, pterygoid, transversum, maxillary and vomer are pulled back to their normal position, and the snout is lowered.

The m. pterygoideus rotates the transversum (and therefore also the maxillary). Thus it deposits the poison fangs back in the "Schleimhauttaschen".

SUMMARY

- 1 The lamina transversalis anterior is present.
- 2 It seems highly likely that the m. retractor vomeris takes part in the emptying of the organ of Jacobson.

- 3 The foramen epiphaniale is absent and the ramus lateralis nasi of the ethmoidal nerve passes over a lateral incisure.
- 4 The lamina orbitonasalis fails to reach the nasal septum posteriorly.
- 5 The a. carotis interna passes directly through a carotid foramen.
- 6 Paired orbitosphenoids are situated internal to the parietals.
- 7 A laterosphenoid separates the n. ophthalmicus profundus V on its medial side from the r. maxillaris V and r. mandibularis V on its lateral side.
- 8 The n. glossopharyngeus passes through a fenestra glossopharyngea interna, situated in the medial wall of the otic capsule.
- 9 A processus dorsalis occurs on the distal end of the columella auris.
- 10 The occipital region does not participate in the formation of the cartilaginous tectum.
- 11 The hypoglossal nerves pass through 2 pairs of foramina in the postero-lateral corners of the exoccipitals.
- 12 The septomaxillary forms a hinge in which the nasal region articulates with the orbital region.
- 13 The prefrontal and postfrontal are the only circumorbital bones present.
- 14 The tabular is the only temporal bone present.

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